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Mathematics. — *Ueber Räume mit verschwindender erster Brouwerscher Zahl.* By PAUL URYSOHN †, rewritten by PAUL ALEXANDROFF. (Communicated by Prof. L. E. J. BROUWER).

(Communicated at the meeting of February 25, 1928).

Unter einem Raum wird im folgenden ein kompakter metrischer Raum R verstanden. Wir setzen voraus, dass die erste Brouwersche Zahl¹⁾ von R verschwindet:

$$\beta^1(R) = 0,$$

d.h., dass man zu jedem $\varepsilon > 0$ ein $\delta > 0$ so finden kann, dass jeder in R liegende eindimensionale δ -Zykel in R ε -homolog Null ist²⁾.

In der vorliegenden Arbeit soll folgender Satz bewiesen werden:

Satz. *Es seien F_1 und F_2 zwei zueinander fremde abgeschlossene Teilmengen von R und $\gamma^0 = (a, b)$ ein zu R gehörendes Punktepaar von der Eigenschaft, dass es zwei diese beiden Punkte in $R - F_1$ bzw. in $R - F_2$ verbindende Kontinuen C_1 und C_2 gibt. Dann gibt es ein Kontinuum C , welches die beiden Punkte a und b in $R - (F_1 + F_2)$ verbindet.*

Mit anderen Worten:

In jedem Raum mit verschwindender erster Brouwerscher Zahl gilt der (klassische)³⁾ Phragmén-Brouwersche Satz.

¹⁾ BROUWER, Invarianz der geschlossenen Kurve, *Math. Ann.*, **72**, (1912), S. 422—425. Bei der Betrachtung von Räumen, die weder ebenen Mengen homöomorph, noch eindimensional sind, ist der Brouwersche Begriff der ε -Abänderung durch den ihm nachgebildeten Begriff der ε -Homologie²⁾ zu ersetzen (in dem von BROUWER a.a.O. explizit behandelten Fall sind beide Begriffe gleichbedeutend). Dies ist die einzige Abänderung des Wortlautes der Brouwerschen Definition der *Vielfachheit der Basis der Zyklisis*, die erforderlich ist, um den Begriff (und zwar nicht nur der ersten, sondern sogleich) der r -ten Brouwerschen Zahl in voller Allgemeinheit zu erhalten. Dieser Begriff ist zum ersten Mal im Anschluss an eine Bemerkung BROUWERS von VIETORIS (*Math. Ann.*, **97** (1927), S. 464, Zeilen 5—10 von oben) explizit formuliert worden.

Siehe in diesem Zusammenhange auch eine vor Kurzem in den Göttinger Nachrichten erschienene Arbeit von ALEXANDROFF („Ueber die Dualität zwischen den Zusammenhangszahlen u.s.w.“, vorgelegt in der Sitzung 25. Nov. 1927), sowie die Arbeiten von FRANKL (Wiener Sitzungsberichte, *Math.-nat. Kl.*, Abt. IIa, Bd. **136**, S. 689, vorgelegt in der Sitzung 15. Dez. 1927) und LEFSCHETZ (*Proceed. Nat. Acad.*, vol. **13**, S. 614 (8. Aug. 1927)), richtig gestellt in *Proceed. Nat. Acad.*, vol. **13**, S. 805 (9 Nov. 1927), weiter ausgeführt *Annals of Math.*, 2. ser., **29**, SS. 232—254 (1928)). Vgl. auch die früheren Arbeiten von ALEXANDROFF (insbesondere *Math. Ann.*, **96** (1926), SS. 520—534 und *Comptes Rendus*, **184**, (21 février 1927), S. 317).

²⁾ Siehe Vietoris, *Math. Ann.*, **97**, S. 458. Es sei an dieser Stelle ausdrücklich erwähnt, dass im folgenden alle der kombinatorischen Topologie entnommenen Begriffe (Rand eines Komplexes, Homologie u.s.w.) im Sinne der Definitionen „modulo 2“ verstanden werden; über diese von ALEXANDER und VELEN herrührende Betrachtungsweise kombinatorischer Begriffe ist von VIETORIS a.a.O. ausführlich referiert worden.

³⁾ Der (klassische) Phragmén-Brouwersche Satz ist von BROUWER (*Math. Ann.*, **71**

Beweis.

Aus den Voraussetzungen unseres Satzes folgt, dass die drei Entfernungen

$$(1) \quad \varrho(C_1, F_1), \varrho(C_2, F_2), \varrho(F_1, F_2)$$

positiv sind; man wähle nun eine positive Zahl $3a$, die kleiner ist, als jede der drei Zahlen (1). Es sei ferner ε eine der einzigen Bedingung $\varepsilon < a$ unterworfenen positive Zahl und $\delta < \varepsilon$ so klein, dass jeder eindimensionale δ -Zykel in R ε -homolog Null ist. Man verbinde jetzt a und b mit je einer aus Punkten von C_1 bzw. C_2 bestehenden δ -Kette ⁴⁾; jede dieser beiden Ketten kann als ein in C_1 bzw. in C_2 (also in R) liegender eindimensionaler Komplex L_1^1 bzw. L_2^1 aufgefasst werden; da diese beiden Komplexe denselben (aus dem Punktepaar $\gamma^0 = (a, b)$ bestehenden) Rand haben, ist ihre Summe ein δ -Zykel Γ^1 , der (vermöge unserer Voraussetzung über die Zahl δ) in R ε -homolog Null ist. Es existiert somit ein durch Γ^1 begrenzter zweidimensionaler δ -Komplex K^2 :

$$(2) \quad K^2 \rightarrow \Gamma^1 \pmod{2}.$$

Man bezeichne jetzt mit Q^2 den Teilkomplex von K^2 , welcher aus allen denjenigen Dreiecken des letzteren Komplexes gebildet ist, deren wenigstens ein Eckpunkt eine die Zahl a nicht übertreffende Entfernung von der Menge F_1 hat. Da Q^2 in $S(F_1, 2a)$ enthalten ist, so ist dieser Komplex zu den beiden Mengen C_1 und F_2 (von denen jede eine Entfernung $> 3a$ von F_1 hat) fremd, insbesondere ist also auch der Rand von Q^2 (den wir mit Δ^1 bezeichnen wollen) zu F_2 fremd, und zwar hat jeder Eckpunkt von Δ^1 eine mindestens a betragende Entfernung von F_2 .

Wir setzen jetzt

$$L^1 = L_2^1 + \Delta^1 \pmod{2}.$$

Aus der obigen Bemerkung und aus der Ungleichung $\varrho(C_2, F_2) > 3a > a$ folgt, dass jeder in L^1 vorkommende Eckpunkt um mehr als a von F_2 entfernt ist; andererseits treten alle "Strecken", die mindestens einen von F_1 um höchstens a entfernten Endpunkt haben, wenn überhaupt in L_2^1 oder Δ^1 , dann sowohl in L_2^1 wie auch in Δ^1 , also nicht in L^1 auf; somit

(1911), SS. 306—308) im § 2 der „Invarianz des n -dimensionalen Gebietes" bewiesen und lautet folgendermassen: „Ist das im n -dimensionalen Koordinatenraum R^n liegende Punktepaar a, b durch keine der beiden zueinander fremden beschränkten abgeschlossenen Mengen F_1 und F_2 voneinander getrennt ⁷⁾, so werden die Punkte a und b auch durch die Vereinigungsmenge $F_1 + F_2$ nicht voneinander getrennt". Wegen Verallgemeinerungen des Phragmén-Brouwerschen Satzes siehe P. ALEXANDROFF, Comptes Rendus, 183 (1926), S. 722 und 184 (1927), S. 575, sowie Fund. Math., II (Auszug aus einem Briefe an Herrn MAZURKIEWICZ).

⁴⁾ Unter einer σ -Kette zwischen zwei Punkten a und b wird (einem von G. CANTOR herrührenden Sprachgebrauch entsprechend) eine endliche Folge von Punkten

$$c_0 = a, c_1, c_2, \dots, c_n, c_{n+1} = b$$

verstanden, die der Bedingung $\varrho(c_i, c_{i+1}) < \sigma, i = 0, 1, 2, \dots, n$, genügt.

sind alle Eckpunkte von L^1 um mindestens α von $F_1 + F_2$ entfernt. Da die Randbildung additiv und Δ^1 ein Zyklus ist, so ist der Rand von L^1 mit dem Rande von L_2^1 , also mit dem Punktepaar (a, b) identisch; es existiert infolgedessen in L^1 ein δ -„Strecken Zug“ der a mit b verbindet.

Wir sind hiermit zu folgendem Ergebnis gelangt:

Zu jedem noch so kleinen $\delta > 0$ gibt es eine aus Punkten von R gebildete δ -Kette, die die Punkte a und b verbindet und um mindestens α von $F_1 + F_2$ entfernt ist.

Man betrachte nun eine gegen Null konvergierende Folge von positiven Zahlen

$$\delta_1, \delta_2, \dots, \delta_i, \dots$$

und es seien

$$(3) \quad \{a = c_0^i, c_1^i, \dots, c_{n_i+1}^i = b\} \quad (i = 1, 2, \dots \text{ in inf.})$$

die zugehörigen δ_i -Ketten; man bezeichne mit Z_i die aus den Punkten von (3) gebildete Punktmenge; da R kompakt ist, so kann man aus der Folge $Z_1, Z_2, \dots, Z_i, \dots$ eine konvergente Teilfolge wählen⁵⁾, deren topologischer Limes C ein Kontinuum ist⁶⁾, welches die beiden Punkte a und b enthält und von der Menge $F_1 + F_2$ eine positive Entfernung $\geq \alpha$ hat. C genügt somit allen Forderungen unseres Satzes.

Korollar. *Es sei R ein Raum mit verschwindender erster Brouwerscher Zahl und C eine abgeschlossene Teilmenge von R , welche die Punkte a und b voneinander trennt⁷⁾, ohne dass es eine abgeschlossene echte Teilmenge von C mit dieser Eigenschaft gibt; dann ist C ein Kontinuum.*

Der Beweis dieser Tatsache ist wörtlich derselbe, wie im Falle, wo R der R^n ist⁸⁾: es genügt zu zeigen, dass die erwähnte Trennungseigenschaft im Brouwerschen Sinne induktiv ist (was aus der Kompaktheit von R in der üblichen Weise folgt), und dann den Phragmén-Brouwerschen Satz anzuwenden.

Da eine ebene abgeschlossene Menge die Ebene dann und nur dann nicht zerlegt⁹⁾, wenn ihre erste Brouwersche Zahl verschwindet, so ist sowohl unser Satz als auch sein Korollar insbesondere auf alle ebenen Kontinuen anwendbar, die in der Ebene nur ein zusammenhängendes Gebiet bestimmen.

⁵⁾ Siehe z.B. URYSOHN, Verhandelingen d. Kon. Akademie Amsterdam, Eerste Sectie, Deel XIII, N^o. 4, S. 35, sowie HAUSDORFF, Mengenlehre (1927), S. 150, Satz VI.

⁶⁾ Siehe URYSOHN, a.a.O. S. 33, Satz III.

⁷⁾ Wir sagen, dass im Raume R eine abgeschlossene Menge F die Punkte a und b voneinander trennt, wenn jedes diese Punkte verbindende Kontinuum mit F gemeinsame Punkte hat. (BROUWER, a.a.O. 3)).

⁸⁾ BROUWER, a.a.O. 3).

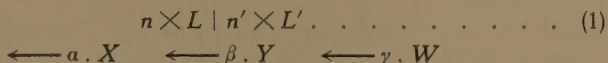
⁹⁾ BROUWER, a.a.O. 1).

Chemistry. — *Osmosis of ternary liquids. General considerations.* VI.
By F. A. H. SCHREINEMAKERS.

(Communicated at the meeting of September 29, 1928).

Congruent, incongruent osmosis and the membrane.

We now consider the osmotic system:



We represent the composition of the liquid L by:

$$x \text{ mol } X + y \text{ mol } Y + (1 - x - y) \text{ mol } W$$

and that of the liquid L' by:

$$x' \text{ mol } X + y' \text{ mol } Y + (1 - x' - y') \text{ mol } W$$

We now cause a small quantity of the substances X, Y and W (viz. a, β and γ mol) to diffuse in the direction of the arrows, consequently from right to left.

The n quantities of L first contain nx mol. X and ny mol. Y ; afterwards there are on the left side of the membrane $n + a + \beta + \gamma$ quantities of liquid, containing $nx + a$ mol. X and $ny + \beta$ mol. Y . The composition of L has changed, therefore, with:

$$\left. \begin{aligned} dx &= \frac{nx + a}{n + a + \beta + \gamma} - x = \frac{(1 - x)a - x\beta - x\gamma}{n + a + \beta + \gamma} \\ dy &= \frac{ny + \beta}{n + a + \beta + \gamma} - y = \frac{-ya + (1 - y)\beta - y\gamma}{n + a + \beta + \gamma} \end{aligned} \right\} . . . (2)$$

We may find the changes dx' and dy' of the right side liquid L' by giving the opposite sign to a, β and γ in (2).

If we represent the Th. d. pot. (thermodynamical potential) of the liquid L by Z , then, its composition changing with dx and dy , this will become:

$$Z + \frac{\partial Z}{\partial x} dx + \frac{\partial Z}{\partial y} dy (3)$$

As there are now $n + a + \beta + \gamma$ quantities of this liquid on the left side, the Th. d. pot. on the left side of the membrane will increase with:

$$(n + a + \beta + \gamma) \left(Z + \frac{\partial Z}{\partial x} dx + \frac{\partial Z}{\partial y} dy \right) - nZ . . . (4)$$

Substituting dx and dy of (2) here, we shall find:

$$- \xi_x a - \xi_y \beta - \xi_w \gamma (5)$$

Here:

$$\left. \begin{aligned} \xi_x &= -Z - (1-x) \frac{\partial Z}{\partial x} + y \frac{\partial Z}{\partial y} \\ \xi_y &= -Z + x \frac{\partial Z}{\partial x} - (1-y) \frac{\partial Z}{\partial y} \\ \xi_w &= -Z + x \frac{\partial Z}{\partial x} + y \frac{\partial Z}{\partial y} \end{aligned} \right\} \dots \dots \dots (6)$$

to the meaning of which we shall refer later on.

If we represent the Th. d. pot. of liquid L' by Z' , then we find in a corresponding way that the Th. d. pot. on the right side of the membrane increases with:

$$\xi'_x \alpha + \xi'_y \beta + \xi'_w \gamma \dots \dots \dots (7)$$

We find ξ'_x , ξ'_y and ξ'_w by giving to all variables in (6) the sign '. Consequently, as follows from (5) and (7), the Th. d. pot. of the total system increases with:

$$(\xi'_x - \xi_x) \alpha + (\xi'_y - \xi_y) \beta + (\xi'_w - \xi_w) \gamma \dots \dots \dots (8)$$

As this total Th. d. pot. cannot do anything but decrease or remain constant, so (8) must be either negative or zero. Consequently α , β and γ may not be taken arbitrarily, but they have to satisfy the condition:

$$(\xi_x - \xi'_x) \alpha + (\xi_y - \xi'_y) \beta + (\xi_w - \xi'_w) \gamma \geq 0 \dots \dots \dots (9)$$

In (3) we have neglected the higher powers of dx and dy ; if we limit ourselves to terms of the second order, we must still add the term:

$$q = \frac{1}{2} (r dx^2 + 2s dx dy + t dy^2)$$

to (3) and consequently a term nq to (5). In the same way it appears that we must still add a term $n'q'$ to (7) and, therefore, still a term $N = nq + n'q'$ to (8). We are able to compute q and q' and, consequently also N ; for our purpose, however, it is not necessary. For our purpose it is sufficient to know the sign of N and, if we consider stable liquids only, this is positive, because q and q' then are positive. Instead of (9) α , β and γ must, therefore, satisfy:

$$(\xi_x - \xi'_x) \alpha + (\xi_y - \xi'_y) \beta + (\xi_w - \xi'_w) \gamma - N \geq 0 \dots \dots (10)$$

in which N is a term of the second order, which is positive for all values of α , β and γ .

Now we shall first take the simple case that only one of the substances e.g. W (water) passes through the membrane; then α and β are zero and system (1) passes into the system:

$$n \times L \mid n' \times L' \longleftarrow \gamma \cdot W \dots \dots \dots (11)$$

Instead of (10) we now get:

$$(\xi_w - \xi'_w) \gamma - C \gamma^2 \geq 0 \quad . \quad . \quad . \quad . \quad . \quad . \quad (12)$$

in which C is positive. We now distinguish 3 cases.

1. $\xi_w > \xi'_w$. As γ^2 is infinitely small with respect to γ , the sign of (12) is defined by the first term; consequently γ must satisfy:

$$(\xi_w - \xi'_w) \gamma > 0 \quad . \quad . \quad . \quad . \quad . \quad . \quad (13)$$

As the coefficient of γ is positive, γ must be positive also. Therefore, in (11) the water diffuses in the direction of the arrow, viz. towards the left.

2. $\xi_w < \xi'_w$. We now see that γ must be negative; now the water diffuses in (11) in a direction opposite to that of the arrow, viz. towards the right.

3. $\xi_w = \xi'_w$. Instead of (12) we now have:

$$-C \gamma^2 \geq 0 \quad . \quad . \quad . \quad . \quad . \quad . \quad (14)$$

As C is positive and γ^2 is also positive for all values of γ , the first part of (14) must always be negative; consequently we can only satisfy (14) by $\gamma = 0$. So no W passes through the membrane and the two liquids are in osmotic equilibrium.

We see from this that it depends on the values of ξ_w en ξ'_w (viz. on their difference) whether water will diffuse and in what direction it will go. Now we call ξ_w the *O.W.A.* (osmotic water-attraction) of the left side liquid and ξ'_w the *O.W.A.* of the right side liquid. If we represent a membrane, through which only W diffuses, by $M(W)$, then we may say, therefore:

water diffuses through a membrane $M(W)$ towards that side, where the *O.W.A.* is the greatest;

if both liquids have the same *O.W.A.*, then no water passes through a membrane $M(W)$.

We now take a liquid g , represented in fig. 1 by point g . We now may put the question: are there any other liquids, which have the same *O.W.A.* as this liquid g ? We then have to satisfy:

$$(\xi_w)_g = -Z + x \frac{\partial Z}{\partial x} + y \frac{\partial Z}{\partial y} \quad . \quad . \quad . \quad . \quad . \quad . \quad (15)$$

The left part represents the *O.W.A.* of the liquid g and has, therefore, a definite value. The right part represents (comp. 6) the *O.W.A.* of the liquid looked for. As its composition (xy) must satisfy (15), it follows:

there exists an infinite number of liquids, which have the same O.W.A. as liquid g ; they are all situated on a curve ab (fig. 1) going through point g ; previously we have called it the isotonic W -curve.

Although the liquids of this isotonic curve may have a very different amount of W , they yet have the same O.W.A. In the systems:

$$L_f | L_g ; L_g | L_h ; L_a | L_b (16)$$

etc., therefore, no water will diffuse through the membrane $M(W)$.

It is clear that there exists an infinite number of isotonic curves; in fig. 1 three of them have been drawn, viz. a_1b_1 , ab and a_2b_2 . All liquids

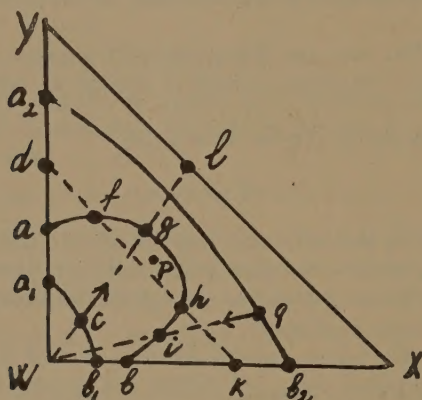


Fig. 1.

of a_1b_1 , therefore, have the same O.W.A., also those of ab and those of a_2b_2 . As we shall see directly, the O.W.A. of the liquids of curve ab , however, is greater than that of curve a_1b_1 , and that of curve a_2b_2 greater again than that of curve ab . Among others these curves have the following properties.

1. Two isotonic curves can never intersect or touch one another.
2. Every straight line, going through point W , intersects an isotonic curve in one point only.
3. The O.W.A. of the liquids of an isotonic curve becomes greater, the farther this curve is situated from point W .
4. The isotonic curves are straight lines in the vicinity of point W ; farther away they are curved and may get all kind of forms.

For the O.W.A. of a liquid is valid:

$$\xi_w = -Z + x \frac{\partial Z}{\partial x} + y \frac{\partial Z}{\partial y}.$$

From this follows:

$$d\xi_w = (xr + ys) dx + (xs + yt) dy (17)$$

If n quantities of liquid take in δn quantities of W , then dx and dy are defined by (2), in which we then have to put $\alpha=0$, $\beta=0$ and $\gamma=\delta n$. We then find for (17):

$$d\xi_w = -(rx^2 + 2sxy + ty^2) \frac{\delta n}{n} \dots \dots \dots (18)$$

As the form, placed between parentheses, is positive, it follows from this: the O.W.A. of a liquid decreases when it takes in water (δn pos.); the O.W.A. increases, when it gives off water (δn neg.).

When in fig. 1 a liquid passes along line lW (viz. starting from l towards W) then its W -amount increases continuously; consequently its O.W.A. decreases; if, however, it passes along line Wl (viz. from W to l) then its O.W.A. increases.

From this we can immediately deduce the properties 1—3, mentioned above.

If we take liquid c of curve $a_1 b_1$ (fig. 1) and liquid q of curve $a_2 b_2$, we have the system:

$$L_c \mid L_q \longrightarrow W \dots \dots \dots (19)$$

in which the right side liquid has a larger O.W.A. than the left side one; consequently through a membrane $M(W)$ water diffuses towards the right. Therefore, liquid c gives off water and moves along line cl in the direction of the arrow in point c ; its O.W.A. increases. The liquid q takes in water and moves along line qW in the direction of the arrow in point q ; its O.W.A. increases. The diffusion of water will continue till both liquids get the same O.W.A., consequently till they reach the same isotonic W -curve. If we assume that this is on curve ab , then, at the end of the osmosis liquid c comes in g and liquid q in i . Consequently system (19) passes into the osmotic equilibrium:

$$L_g \mid L_i \dots \dots \dots (20)$$

in which no W diffuses anymore¹⁾.

All that has been deduced above for the substance W (water), obtains also for every arbitrary other substance.

If e.g. only the substance X passes through the membrane, then system (1) passes into:

$$n \times L \mid n' \times L' \longleftarrow a \cdot X \dots \dots \dots (21)$$

(10) now passes into:

$$(\xi_x - \xi'_x) a - Aa^2 \equiv 0 \dots \dots \dots (22)$$

In the same way as described above, it follows from this that it depends on the values of ξ_x and ξ'_x whether the substance X will diffuse

¹⁾ For positive, negative, normal and anormal osmosis in those systems, compare: F. A. H. SCHREINEMAKERS, Osmosis of liquids. The Journal of General Physiology. Vol. 11, N^o. 6, pp. 701—713 (1928).

and in what direction it will go. We shall call ξ_x and ξ'_x the O.X.A. (osmotic X-attraction) of the liquids.

It appears in the same way that it depends on ξ_y and ξ'_y whether the substance Y will diffuse and in which direction it will go; we shall call this the O.Y.A. of the liquids.

If we take an arbitrary substance S and a membrane $M(S)$, viz. a membrane which only lets through this substance S, then we may say, therefore:

substance S diffuses through a membrane $M(S)$ towards that side, where the O.S.A. is greatest;

if both liquids have the same O.S.A., then no S passes through a membrane $M(S)$;

there exists an infinite number of liquids, which have the same O.S.A. as a given liquid.

In fig. 2 we find three curves, passing through point 1. Curve ab is an isotonic W-curve; it represents the liquids which have the same O.W.A. as liquid 1. Curve cd is an isotonic X-curve; it represents the

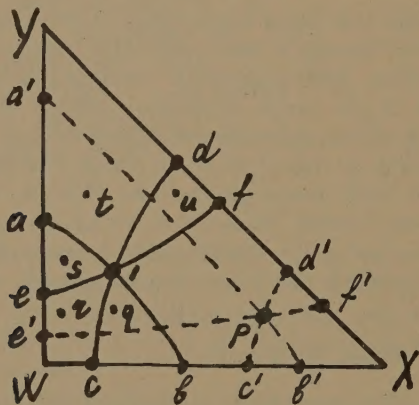


Fig. 2.

liquids, which have the same O.X.A. as liquid 1. Curve ef is an isotonic Y-curve; it represents the liquids which have the same O.Y.A. as liquid 1.

Above we have seen that there exists an infinite number of isotonic W-curves; consequently there exists an infinite number of isotonic X- and Y-curves. Of course the same properties as have been discussed above for the W-curves, obtain also for them. Therefore, we find among other things:

the O.X.A. (O.Y.A.) of the liquids of an isotonic X-curve (Y-curve) is greater the further those curves are away from point X (Y).

When the three dotted curves also represent isotonic curves, then we have, therefore:

the liquids of curve ab have a smaller $O.W.A.$ than those of curve $a'b'$;

the liquids of curve cd have a greater $O.X.A.$ than those of curve $c'd'$;

the liquids of curve ef have a smaller $O.Y.A.$ than those of curve $e'f'$.

Among other things it follows from the above that liquid 1 has a greater $O.X.A.$, but a smaller $O.Y.A.$ and $O.W.A.$ than liquid p . We represent this by:

$$\begin{array}{ccccc} & L_1 | L_p & \text{fig. 2} & & \\ O.X.A. & O.Y.A. & O.W.A. & \left. \begin{array}{c} \longleftarrow \quad \longrightarrow \quad \longrightarrow \end{array} \right\} & . . . \quad (23) \end{array}$$

in which, therefore, the arrows point towards that side of the membrane, where the osmotic attraction is greatest. Consequently those arrows also indicate the direction in which a substance diffuses through a membrane, which transmits this substance only.

Consequently X diffuses through a membrane $M(X)$ towards the left, Y through a membrane $M(Y)$ and W through a membrane $M(W)$ towards the right.

We now take the liquids 1 and q of fig. 2. If we imagine the three isotonic curves also drawn through q , then we see that liquid 1 has a larger $O.X.A.$ and a larger $O.W.A.$, but a smaller $O.Y.A.$ than liquid q . We represent this by:

$$\begin{array}{ccccc} & L_1 | L_q & \text{fig. 2} & & \\ O.X.A. & O.Y.A. & O.W.A. & \left. \begin{array}{c} \longleftarrow \quad \longrightarrow \quad \longleftarrow \end{array} \right\} & . . . \quad (24) \end{array}$$

Consequently we see that X diffuses through a membrane $M(X)$ and W through a membrane $M(W)$ towards the left and Y through a membrane $M(Y)$ towards the right.

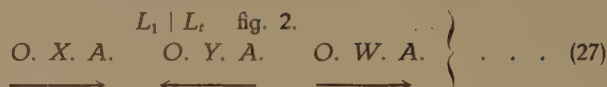
For the liquids 1 and r we find:

$$\begin{array}{ccccc} & L_1 | L_r & \text{fig. 2} & & \\ O.X.A. & O.Y.A. & O.W.A. & \left. \begin{array}{c} \longrightarrow \quad \longrightarrow \quad \longleftarrow \end{array} \right\} & . . . \quad (25) \end{array}$$

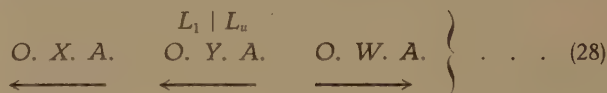
For the liquids 1 and s obtains:

$$\begin{array}{ccccc} & L_1 | L_s & \text{fig. 2} & & \\ O.X.A. & O.Y.A. & O.W.A. & \left. \begin{array}{c} \longrightarrow \quad \longleftarrow \quad \longleftarrow \end{array} \right\} & . . . \quad (26) \end{array}$$

For the liquids 1 and t we find:



and for the liquids 1 and u :



We shall call those systems (23)–(28) the systems $p, q \dots u$.

We now take a system:



in which a membrane $M(XYW)$ or $M(3)$ viz. a membrane which transmits the three substances. Then the question arises:

in which direction will each of the substances X, Y and W now go through the membrane?

We shall begin by assuming that every substance can diffuse as well towards the left as towards the right; then we can distinguish the eight cases of scheme I (we are shortly going to refer to the letters p, q etc. placed between parentheses). We call each of those cases a $D. T.$ („diffusion-type”).

In order to simplify a further discussion, we shall call the direction, in which X diffuses through a membrane $M(X)$ (consequently from a smaller towards a greater $O.X.A.$) the “congruent” direction of X . We call the opposite direction (consequently from a greater towards a smaller $O.X.A.$) “incongruent”. We act in the same way with Y, W and other substances.

We now call a diffusion-type:

“congruent” when all substances diffuse congruently;

“incongruent” when all substances diffuse incongruently.

“mixed” when at the same time congruent and incongruent directions occur.

We shall first consider the system p (viz. 23). As in (23) the arrows indicate the side, where the osmotic attraction is greatest, they indicate the congruent direction of each of the substances X, Y and W . If we compare these directions with those of scheme I, we see:

Nº. 4 represents the congruent and Nº. 5 the incongruent $D. T.$ of system p .

In order to indicate that Nº. 5 is the “incongruent” $D. T.$ of system p , the letter p has been put here between parentheses.

If in scheme I we imagine the sign o to be placed on the right side of each arrow, indicating an incongruent direction, we get scheme Ip.

SCHEME I.

	<i>X</i>	<i>Y</i>	<i>W</i>
1.	←	←	←
2. (<i>r</i>)	←	←	→
3. (<i>t</i>)	←	→	←
4. (<i>s</i>)	←	→	→
5. (<i>p</i>)	→	←	←
6. (<i>q</i>)	→	←	→
7. (<i>u</i>)	→	→	←
8.	→	→	→

SCHEME *I_p*

	<i>X</i>	<i>Y</i>	<i>W</i>
1.	←	← o	← o
2.	←	← o	→
3.	←	→	← o
4.	←	→	→
5.	[→ o	← o	← o]
6.	→ o	← o	→
7.	→ o	→	← o
8.	→ o	→	→

SCHEME *I_q*

	<i>X</i>	<i>Y</i>	<i>W</i>
1.	←	← o	←
2.	←	← o	→ o
3.	←	→	←
4.	←	→	→ o
5.	→ o	← o	←
6.	[→ o	← o	→ o]
7.	→ o	→	←
8.	→ o	→	→ o

This shows quite clearly that *N*⁰. 4 is the congruent and *N*⁰. 5, placed between parentheses, the incongruent *D.T.* of system *q*. The other *D.T.* are mixed; in 2, 3 and 8 one substance goes incongruently through the membrane, in 1, 6 and 7 two substances.

In system *q* (viz. 24) the arrows also indicate the congruent directions of the substances *X*, *Y* and *W*; consequently *N*⁰. 3 of scheme I represents the congruent *D.T.* of this system and *N*⁰. 6 the incongruent *D.T.* This has again been indicated scheme I by placing the letter *q* between parentheses with *N*⁰. 6. For this system *q* we now find the scheme *I_q*.

If we only pay attention to the fact whether a system goes through the membrane towards the left or towards the right, the *D.T.* of scheme *I_p* are the same as those of *I_q*. If, however, we also take into consideration the "congruentness" or "incongruentness" of these directions, then there is a great difference.

For instance in *N*⁰. 1 of *I_p* substances do go through the membrane in the same direction as in *N*⁰. 1 of *I_q*; but in the first case *Y* and *W* diffuse incongruently and in the second *Y* only.

For the other *D.T.* we find corresponding differences.

In a corresponding way we find the congruent and consequently also the incongruent *D. T.* of the other systems. In (30) we find them united for all systems.

system	<i>p</i>	<i>q</i>	<i>r</i>	<i>s</i>	<i>t</i>	<i>u</i>	
congr. <i>D. T.</i>	4	3	7	5	6	2	} (30)
incongr. <i>D. T.</i>	5	6	2	4	3	7	

We also see this in scheme I; the letter *r*, placed between parentheses with $N^0. 2$, namely indicates that $N^0. 2$ is the incongruent *D. T.* of system *r*, etc. In the same way as this has been done above for the systems *p* and *q*, the reader also may deduce a scheme for each of the other systems and indicate the incongruent directions in it by the sign 0.

From scheme I or (30) appears among other things:
 the composition of the two liquids determines which of the 8 *D. T.* is congruent (incongruent);
 all *D. T.* can be congruent (incongruent) except 1 and 8.

So for each osmotic system, having a membrane *M*(3), eight different *D. T.* exist; we must, however, put the question whether they all are possible.

For this purpose we take system (1), in which α mol. *X*, β mol. *Y* and γ mol. *W* diffuse towards the left. When α is negative, *X* goes in the opposite direction, when β is negative, *Y* goes in the opposite direction, and when γ is negative, *W* goes in the opposite direction. If we pay attention to the signs, which we can give to α , β and γ , we get the eight *D. T.* of scheme I.

We have already seen, however, that α , β and γ can not be taken quite arbitrarily, but have to satisfy (10). In this we put:

$$\xi_x - \xi'_x = K_x ; \quad \xi_y - \xi'_y = K_y ; \quad \xi_w - \xi'_w = K_w (31)$$

As long as the three first terms together do not amount to zero, the sign of (10) will be determined by these terms. If we put, therefore:

$$K = \alpha K_x + \beta K_y + \gamma K_w (32)$$

then α , β and γ must satisfy:

$$K > 0 (33)$$

When the three terms of *K* are positive, then, (33) has consequently been satisfied; when one or two terms are negative, α , β and γ may yet be chosen either so large or so small that *K* will be positive; when each of the three terms is negative, however, *K* is always negative. Consequently we are not able to satisfy (33) when at the same time:

$$\alpha K_x < 0 ; \quad \beta K_y < 0 ; \quad \gamma K_w < 0 (34)$$

When aK_x is negative, then a and K_x must have opposite signs. If we consider the value of K_x in (31), we can distinguish two cases.

1. $\xi_x > \xi'_x$ and $a < 0$. Consequently the *O.W.A.* is larger on the left side of the membrane than on the right side; therefore, the congruent direction of X is towards the left; [consequently through a membrane $M(X)$, X would go towards the left]. As, however, a now is negative, X diffuses towards the right, i.e. incongruently.

2. $\xi_x < \xi'_x$ and $a > 0$. Now the congruent direction of X is towards the right. As, however, a is positive now, X diffuses towards the left, consequently once more incongruently.

$aK_x < 0$ means, therefore, that the substance X diffuses incongruently;

$\beta K_y < 0$ and $\gamma K_w < 0$ have the same meaning for Y and W . Consequently (34) means that X , Y and W diffuse incongruently at the same time. Hence follows:

all diffusion-types are possible, except the incongruent.

From scheme I or (30) appears, therefore:

in system p all *D.T.* are possible, except $N^0. 5$;

in system q all, except $N^0. 6$;

in system r all, except $N^0. 2$; etc.

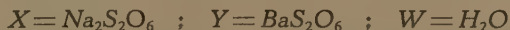
For this reason $N^0. 5$ in scheme I_p and $N^0. 6$ in scheme I_q have been placed between parentheses.

Now we may say:

the composition of the liquids determines which of the diffusion-types is incongruent and, therefore, not possible;

the nature of the membrane determines which of the 7 other *D.T.* will occur.

We have been able to demonstrate this influence of the membrane experimentally in some cases, e.g. in an osmotic system in which the liquids consisted ¹⁾ of:



and of course had a special composition. Through a membrane, made of collodion three substances diffused, according to:



Through a membrane, made of collodion, in which a little $Cu_2 Fe (CN)_6$ had been deposited, they diffused, however, according to:



Consequently the water diffuses through the two membranes in opposite directions; so one of these directions is incongruent.

We also found this in this system, when one of the liquids had an other composition.

¹⁾ Comp. for this system: Exp. II and III.

Also in a system¹⁾, in which the liquids consist of $X = \text{NH}_4\text{Cl}$, $Y = \text{ammonium-succinate}$, $W = \text{H}_2\text{O}$, the *D.T.* depended on the membrane. The substance namely diffused according to (35) through a membrane: *a.* made of collodion; *b.* of a pig's bladder; *c.* of cellophan. According to (36) they diffused, however, through a membrane; *d.* made of collodion, in which a little $\text{Cu}_2\text{Fe}(\text{CN})_6$ had been deposited; *e.* of a pig's bladder, which had been treated in a special way; *f.* of parchment.

So here again it appears that water diffuses through some membranes towards the left and through other membranes towards the right.

We are able to extend the foregoing considerations to membranes, which transmit n substances; among other things we then find:

there exist 2^n diffusion-types;

the composition of the two liquids determines which *D.T.* is incongruent and consequently can not occur;

the nature of the membrane determines which of the $2^n - 1$ other *D.T.* occurs.

Consequently if we take two liquids, containing e.g. five diffusing substances, then the diffusion may take place according to 32 types. If the two liquids are given a special composition, the membrane will determine which of the 31 possible *D.T.* will occur.

If, therefore, only the directions are known in which each of these substances passes through a membrane $M(1)$ [viz. the substance X through a membrane $M(X)$, the substance Y through a membrane $M(Y)$, etc.], we know only very little. For this enables us to find the incongruent *D.T.* only, viz. that, according to which the substances cannot diffuse. The nature of the membrane now determines which of the 31 other *D.T.* will occur.

If besides we bear in mind that during the osmosis a membrane may change its nature and consequently its *D.T.* under all kinds of influences [e.g. the influence of the diffusing substances, age, hysteresis etc.]; we need not be surprised sometimes to see diffusions occur in vegetable or animal tissues, which perhaps were not expected, or when the direction of the diffusion of some substances should at times change in them.

Leiden, Lab. of Inorg. Chemistry.

(To be continued.)

¹⁾ This system will be published later on.

Anatomy. — *A Gland-like Ependymal Structure in the Brain.* By H. H. CHARLTON. University of Missouri School of Medicine and Central Institute for Brain Research, Amsterdam, Holland. (Communicated by Dr. C. U. ARIËNS KAPPERS.)

(Communicated at the meeting of September 29, 1928).

Dr. ARIËNS KAPPERS, '21, has called attention to a modified ependyma lining the walls of the ventral thalamus, beginning just behind the level of the commissura posterior and extending caudally to end under the tuberculum posterius. As the area had a rich blood supply and since in the ventricle adjacent to the specialized region he observed an albuminouslike substance, KAPPERS considered it a secreting organ assisting in the production of cerebro-spinal fluid. He observed the modified area in the Teleost, *Monopterus javanensis*, in various reptiles, in a bird, and finally in the opossum and the dog.

A chance observation of this region in the rockling, *Motella mustela*, where the morphology is much more typically gland-like than in the forms mentioned by KAPPERS, led me to undertake a more extended study, first to find out how general was its occurrence, secondly to note its morphological variations, and lastly to find more evidence regarding its glandular structure and if possible to learn how its secretory products reached the ventricular cavity.

The material for this work consisted of some thirty odd brains prepared by the writer at the Anatomical Laboratory of the University of Missouri¹), and in addition there was available for study the splendid slide collection of the Central Institute for Brain Research, Amsterdam, Holland.

As a routine method the brains were formalin-fixed, sectioned serially twenty to twenty-five microns in thickness and stained in Weigert's, Weigert-Pal's, Delafield's, or Heidenhain's iron haematoxylin. It is obvious that some cytological detail will be found wanting due to the thickness of the sections and to the fact that formalin is not the ideal fixative for such detail.

Outside of the work of KAPPERS already referred to comparatively few investigators have noted this modified ependyma. HOOGENBOOM, '28, in work just published has described it in *Polyodon spathula* where it seems to have, according to her report, a large frontal extension even into the forebrain. RENDALL ('24) found it in the chick brain as early as eight days

¹) I am indebted to the United States Bureau of Fisheries, Woods Hole, Massachusetts for assistance in securing much of this material.

after hatching. It helps to form, both in the embryo and adult, a slight groove or depression, the concavity of which, is directed toward the ventricle. He calls attention to the cells of the stratum cellulare lying under the thickened ependyma which are clumped together and stain more deeply than usual.

Fig. 1.



Fig. 1.

Raja sp. A transverse section through the modified ependymal area and the infundibulum.

holds the same position as the highly modified ependymal region in the selachians which will be described later. They speak of the lower



Fig. 2.

Raja sp. Drawing of the modified ependymal region shown in figure 1 under higher magnification. In a number of crypts a cuticular membrane is quite evident and, located directly beneath it, a nuclei-free area. In the ventricle itself there is an albuminous or homogeneous substance giving the appearance of secretory material.

tuberculum as being characterized by a poorly developed ependyma, below which there are a number of lymphatic cavities. This area, however, is near the region where the ependyma of the hypothalamus joins that of the mid-brain.

In the Elasmobranch fishes a most interesting structure, located just caudo-ventral to the tuberculum posterius, presents itself (fig. 1 and 2). Here the ependyma is folded to form a series of crypts or pockets appearing in transverse section like a rosette. The ependyma is stratified or pseudo-stratified, much thicker than usual and frequently shows a lighter staining area just beneath its cuticula, while in the ventricle itself a homogeneous sort of débris is almost always to be seen.



Fig. 3.

Motella mustela. Transverse section of the infundibulum taken in front of figure 4.

A young specimen of *Raja* has been used for the illustrations in figures 1 and 2 in the present paper, but the same general structure is found in the adult skate, hammerhead shark, sand shark, and the dogfish. In the young *Raja* a single cross-section shows perhaps fifteen crypts, but this does not represent nearly the total number since they extend not only dorsally and laterally but also rostrally and caudally. They are often covered on their ventricular surfaces by a considerable albuminous precipitate. The number of crypts seems greater in the adult *Raja* than in the young specimen. The thickened ependyma extends nearly to the floor of the hypothalamus in a rather close relationship to the beginning of the hypophysis. Whether these crypts represent the recessus mammillaris of *Ceratodus* or that of Teleost fishes cannot perhaps be answered with certainty, but their relationship to the tuberculum posterius would be in favour of this idea.

In Teleosts the modified ependyma begins just behind the posterior commissure and is visible particularly in the ventricular lining of the most

dorsal part of the ventral thalamus immediately underneath the sulcus medius. I can confirm the observation of KAPPERS that it is

never continuous with the well known high ependymal cells which in most forms (Studnicka, '00) lie under the commissura posterior. From its anterior end it bends ventrally and caudally into the hypothalamus where turning laterally it usually forms a shallow basin-like concavity in the roof of the ventricle of the hypothalamus.

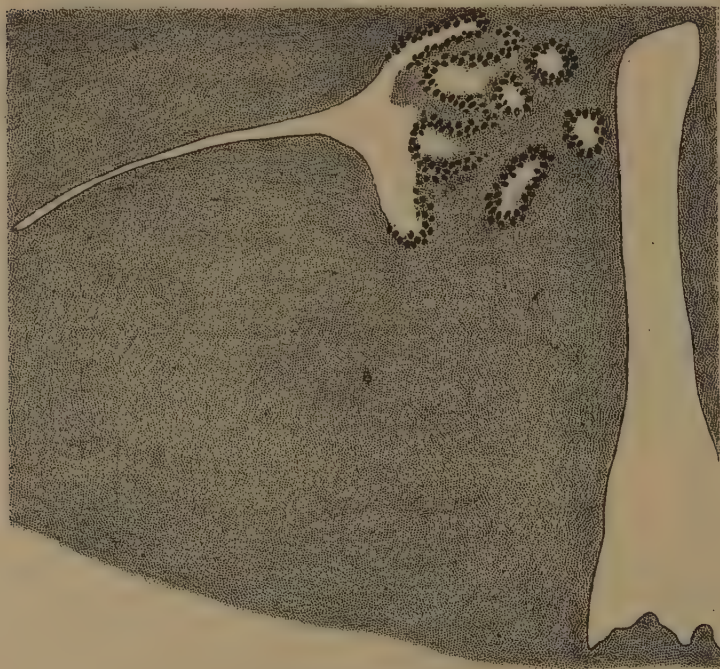


Fig. 4.

Motella mustela. Transverse section of the lateral hypothalamic ventricle.

Occasionally as in *Motella mustela* (figs. 3 and 4) a much more complicated structure is to be seen. Here the region about the entrance into the lateral hypothalamic ventricle forms numerous crypts which are strikingly gland-like. Only the highly modified ependyma is included in the drawings and here one sees a dozen or more crypts pointing in various directions as indicated by their appearance in cross sections. In another slide of *Motella mustela* (fig. 5) the crypts are reduced to some three or four on either side and they are much shallower, but the ependyma is somewhat thicker, showing some four or five nuclei in a section through a crypt wall. Here again cell walls are not visible, but histologically the area appears as in *Raja* (figs. 1 and 2). I have attempted to indicate in

figure 5 the excellent blood supply which this modified ependyma possesses. Just why so much variation in the crypts should occur in the same species is not easy to explain. Perhaps it is a true variation or again it may be due



Fig. 5.

Motella mustela. One of the gland-like crypts under high magnification. Note the stratified or pseudostratified ependyma and its excellent blood supply. Bl. V., blood vessels.

to difference in the development of the individual in as, Elasmobranchs it was noted that the older specimens possessed a more highly developed crypt-like arrangement. The thickened ependyma in *Motella mustela* is not so conspicuous in the ventro-caudal part of the hypothalamus as in other fishes.

The king-fish, *Menticirrhus americanus* (fig. 6), presents a slightly different picture. Just anterior to the level of the tuberculum posterius two very deep glandular-like crypts extend upwards to meet the modified ependyma of the dorsal part of the ventral thalamus, cutting off a wedge shaped portion of the thalamus between the two limbs. The cells lining the crypts show a slighter staining homogeneous border which may represent a stage in the secretion process. There are no tubular glands or crypts as found in *Motella* but there is a shallow inverted basin arrangement in the roof of the lateral hypothalamic ventricle so common in most teleosts.

The caudo-ventral limits of the modified ependyma are usually not easily defined with any degree of certainty, but in some slides of the minnow.



Fig. 6.

Menticirrhus americanus. A transverse section illustrating the common arrangement of the secretory ependyma forming the roof of the lateral hypothalamic ventricles. It gives the appearance of an inverted shallow basin. Note the formation of two deep crypts with a tongue of tissue between. They unite with the modified ependyma of the normal part of the ventral thalamus a few sections rostrally. Tr. G. T., tractus griseo-tuberis.

Gambusia affinis, (figs. 7 and 8), cut in the horizontal plane and stained with HEIDENHAIN's iron haematoxylin, the thickened ependyma tenaciously retained the stain and here the thickened ependyma could not be traced to be continuous with that lining the mammillary recess. It is possible that the recess may really be compared to a tubular gland.

In the reptiles the modified ependyma is clearly differentiated from the ordinary single layered type. In *Lacerta agilis* (figs. 9 and 10) it begins



Fig. 7.

Gambusia affinis. Horizontal sections through the hypothalamus. Modified ependyma seems to be continuous caudo-ventrally with the recessus mammillaris. Tr. G. T., tractus griseotuberis; Mam. Recess, mammillary recess; Lat. Hyp. Lobe, Lateral hypothalamic lobe.

a little anterior as contrasted with the Teleosts, at, or a little in front of, the level of the habenular commissure, and is located on either side of the thalamic ventricle. This modified area is very definitely set off from the ciliated cuboidal ependymal cells by blood vessels entering at either end, and by a thickening of the area itself. The nuclei of its cells are arranged in rows assuming a stratified or pseudostratified condition. On the ventricular side the ependyma forms a slight concavity occupied by a homogeneous nuclei-free substance, presumably the products of these cells.

Tracing the area caudally it retains the same size dorso-ventrally but holds in each caudal section a more ventral position until it reaches and lines a widened ventricular area in the hypothalamus. There is no true

lateral hypothalamic ventricle in *Lacerta* but this pouch-like widening of the hypothalamic ventricle may represent it.

In *Pelias berus* (fig. 11), the common viper of Europe, the modified ependymal area is to be found in the same general location as has been already described in the lizards, only here one finds what seems like a bridge



Fig. 8.

Gambusia affinis. Horizontal sections through the hypothalamus. Modified ependyma seems to be continuous caudo-ventrally with the recessus mammillaris. Tr. G. T., tractus griseotuberis; Mam. Recess, mammillary recess; Lat. Hyp. Lobe, Lateral hypothalamic lobe.

connecting the walls of the thalamus. On closer examination this proves to be a secretion product plus many scattered freed nuclei. The fact that one or more blood vessels cross here from side to side helps to give the impression of a definite connecting strand of brain tissue. This has been formed by the breaking down of the ventricular limiting cuticula here and there, and the desquamation of the inner ends of the modified cells. In the process quite a number of nuclei are included. One notices a definite border in some places and in other places the cuticula has disappeared leaving a depression where cell substance has passed into the ventricle. I am convinced that not only in the snakes but also in the other vertebrates studied the secreting process is a similar one.

In the birds the modified ependyma is not so pronounced as in the reptiles and is chiefly related to the dorsal portion of the ventral thalamus. In the English sparrow, *Passer domesticus* (figs. 12 and 13) one recognizes the stratum cellulare internum referred to by RENDALL lying directly beneath the modified area. The large blood vessels found in the fishes and



Fig. 9.

Lacerta agilis. A transverse section to show the position of the modified ependyma.

reptiles running in the ependyma and on its surface are much less conspicuous in the birds. I have not studied the brain of the common pigeon, *Columba domestica*, but from a photograph of the gland region sent me by Dr. WAYNE T. ATWELL, the structure is quite similar.

According to Patten ('12) in his "Evolution of the Vertebrates", the stomadaeum of the arachnids, representing the ectodermal part of the invertebrate foregut, has become incorporated into the brain of the vertebrates. He states, page 60:

"When the mouth of the arachnids was shut off from the exterior by the backward overgrowth of the rostrum and the optic lobes, and by the closing up of the cerebral

vesicle, the stomodaeum and the adjacent ectoderm remained in the vertebrates as the epithelial lining of the third ventricle and the adjoining chambers; and the opening through the floor of the brain, which served as a passageway for the old oesophagus, remained as the infundibulum. The inner end of the stomodaeum that protrudes through the infundibulum, became the sacci vasculosi; the lateral stomodaeal ganglia, the lobi inferiori; and the stomodaeal commissure, the anlage of the cerebellum. The median haemal portion of the cheliceral neuromere, which is the principal center for the olfactory, gustatory, and stomodaeal impulses, corresponds with the hypothalamic region, while the cheliceral lobes and the cerebral association cells mark the beginning of the thalamus."

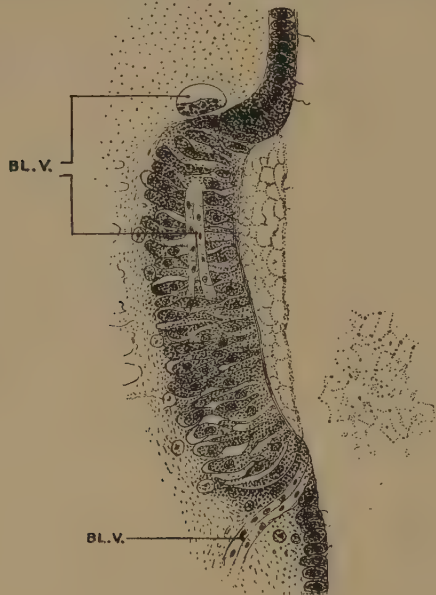


Fig. 10.

Lacerta agilis. The modified area from figure 9 under higher magnification. Note the homogeneous substance in the concavity of the area and in the ventricle. The region is well supplied with blood vessels which tend to reach the gland at its junction with the normal cuboidal ependyma. BL. V., blood vessels.

The region where I have found the modified ependyma corresponds to the caudal portion of the stomodaeal derivative. If Patten's theory is the true one it would help to explain the presence of a secreting ependyma in the diencephalon. In connection with this it may be recalled that WISLOCKI and PUTNAM ('24) consider the areae postremae as a region where fluids pass from the blood stream into the cerebrospinal fluid of the fourth ventricle. According to Patten's conception this area is located in relation to the rostral portion of the stomodaeal derivative.

It is to be noted that the modified ependyma is found in the Elasmobranchs most prominent near what EDINGER ('08) and HOLMGREN and

VAN DER HORST ('25) call the mammillary recess. It occupies a much more posterodorsal place than either the lateral hypothalamic recess or the mammillary recess in the teleosts, and the invaginations are directed dorsally more than laterally. It is located just behind the tuberculum



Fig. 11.

Pelias berus. Transverse section. The cuticular membrane of the modified area seems to disappear in places and the underlying tissue to slough off into the ventricle which in this brain is practically occluded by it. Blood vessels are seen to pass from side to side in the secretory material. BL. V., blood vessels.

posterius. In considering the homology of this recess in Elasmobranchs with the mammillary recess of bony fishes, it is interesting that in the latter the recess seems related to the hypothalamic floor rostral to the infundibulum and saccus vasculosis instead of the more dorsal position in such forms as the skates and sharks. In the teleosts the ependymal development reaches its maximum at the junction of the thalamic ventricle with the lateral hypothalamic recess although having its anterior limits farther rostral and dorsally. The reptiles show what seems to be the most active part of the modified ependyma lining the thalamic ventricle but it can be traced backward to line the hypothalamic widening as well. The position in the birds is still more restricted to the dorsal part of the ventral thalamus, and in the Opossum and the dog the gland-like ependyma is still more reduced, according to KAPPERS (l.c. Vol. II, p. 889).

It would appear, therefore, that the modified area loses its complexity and actually becomes reduced in size as one goes up the phylogenetic scale, and also the point of highest development is more dorso-rostally in the higher



Fig. 12.

Passer domesticus. Cross section. The modified area under low power.



Fig. 13.

Passer domesticus. Area between dotted lines in figure 12 shown under higher magnification.

forms. Only Polyodon seems to be an exception for Miss HOOGENBOOM reports the modified area as extending into the forebrain. The indications are that coincident with these phylogenetic changes there is a reduction as well in the physiological significance of the modified area as one ascends the vertebrate scale.

It would have been most satisfactory if it had been possible to present physiological evidence of the glandular character of the modified ependymal region and since WISLOCKI and PUTMAN ('24) reached the conclusion that the areae postremae acted as an intermediate structure for the conveyance of fluids from the blood to the cerebrospinal fluid, I tried the method used by them, i.e., the procedure described by WEED ('14) of injecting a one or a one and a half per cent solution of potassium ferrocyanide and iron ammonium citrate in RINGER solution intravenously and fixing in acidulated formalin. This precipitates the ferric ferrocyanide (Prussian blue) wherever it happens to be present.

They state that in cats they never found the blue granules anywhere else in the brain but in the areae postremae.

The method used by the writer was to inject this solution directly into the heart at a rate slow enough so as not to interfere with its contractions. Some hours afterwards the animal was killed and fixed. In no case in turtles, lizards, or alligators did blue granules appear either in, the modified ependyma or in the ventricles immediately adjacent to it, although contrary to the findings of WISLOCKI and PUTNAM ('24) in cats, granules were present in large numbers in the neural part of the hypophysis, a description of which will appear in a latter publication. As, however, not every secretory surface shows the transmission of the blue granules after this experiment it does not seem to prove that the surface should not be secretory. Indeed its features as a secretory region are so evident and so constant in all the vertebrates that I can hardly doubt this.

In the region of this ependyma an unmyelinated fiber tract occurs. HOLMGREN ('20, page 291) describes it under the name of *tractus griseo-tuberis* as follows: "Er entspringt in der ventrikulären Ganglienzellschicht der Ventrikelwand dorsal und etwas vor dem Nucleus posterior tuberis. Er erstreckt sich anfangs längs der Ventrikelpendymes nach unten und hinten bis zur Decussatio nervi sacci vasculosi. Hier biegt das Bündel bogenförmig seitwärts und nach hinten, um dorsal und vor dem Recessus lateralis hypothalamicus zu enden."

I observed the same tract in various Teleosts (fig. 7 and 9 Tr. G. T.), extending from directly under the most dorso-rostral portion of the modified ependyma, running parallel to the ependymal wall to the level of the lateral hypothalamic ventricles and seems to end partly in the ependyma forming the roof, while other fibres of this bundle passing behind the lateral recess terminate in relation to the ependyma of the recessus mammillaris.

CONCLUSIONS.

A distinct secretory ependyma occurs in the thalamus of fishes, reptiles, birds, and mammals. It is largest in fishes, then decreases in reptiles and becomes much smaller in the higher vertebrates.

The region is largely supplied with blood vessels which may reach the ventricular surfaces and some of which run in the ventricle itself. Its blood supply decreases notably in birds.

The function of the organ has probably to do with the constitution of the ventricular fluid. The structure in addition to many blood vessels may receive amyelinated nerve fibers from the ventral infundibular areas.

Why this secretory ependyma is so much larger in fishes than in other animals and so small in the highest vertebrates I do not know. It may be that this is connected with life in water.

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Anatomy.— *The Phylogenetic Development of the Substantia Gelatinosa Rolandi*. Part. I. Fishes. By E. KEENAN, M. B., National University of Ireland. (From the Central Dutch Institute for Brain Research, Amsterdam.) (Communicated by Dr. C. U. ARIËNS KAPPERS.)

(Communicated at the meeting of October 27, 1928.)

When we examine a transverse section of the spinal cord of a higher vertebrate we can at once distinguish in the posterior horns certain well-marked areas. In man three subdivisions are described, the relations being as follows: the body of the posterior horn proper occupies the most central position, and is in direct continuity with the anterior horn ventrally; posterior to the body of the horn, and surrounding its extremity like a cap or cortex (KAPPERS, 1914) is the substantia gelatinosa Rolandi; extending from this region to the surface of the cord (the bottom of the postero-lateral sulcus) is Lissauer's marginal zone. This relationship exists throughout the cord, from the medulla oblongata above, where the gelatinous substance of the cord is continuous with a similar structure in relation to the descending root of the fifth cranial nerve, to the conus medullaris below.

The gelatinous substance has a closely massed homogeneous or jelly-like appearance, from which it derives its name. It is practically devoid of myelinated fibres, so that on treating by the Weigert-Pal method, especially if counterstained with paracarmine, it is clearly distinguishable from the rest of the gray matter.

Lissauer's marginal zone, with similar staining, is seen to contain widely separated fine and medium-sized medullated fibres. In addition, small nerve cells, and occasionally larger elements are present.

CAJAL (1909, 1911) attributes the gelatinous appearance of the substance to the rich network of dendrites of the small cells which crowd the area. These dendrites branch mainly in one level, parallel to the posterior surface of the cord. They rarely extend into the gray substance of the posterior horn proper.

The substantia gelatinosa, together with Lissauer's marginal zone, which is believed to be closely related to it functionally, has been extensively studied in higher vertebrates (HATSCHEK in the seal, 1896; DEXLER in the elephant, 1907; SANO in mammals, 1909; RANSON in man, Rhesus monkey, the cat, the rabbit, the albino rat and the guinea pig, 1913, 1914; etc.), and its form and position pretty well described. Researches in this direction in lower forms seem, however, to be almost entirely wanting, as substantia gelatinosa has not been recognised in the posterior horns, or, at any rate, has never been properly described as such.

In the following pages I set down the results of my observations in fishes, as part of a general phylogenetic survey.

The specimens used were from the large collection at the Central Dutch Institute for Brain Research, Amsterdam. The following is a list of the species examined during the progress of this section of the work :

- Amphioxus lanceolatus
- CYCLOSTOMES
 - Petromyzon fluviatilis
- GNATHOSTOMES
- SELACHIANS
- SHARKS
 - Hexanchus griseus
 - Acanthias vulgaris
 - Spinax niger
- RAYS
 - Raja clavata
- HOLOCEPHALIANS
 - Chimaera monstrosa
- GANOIDS
 - Calamoichthys calabaricus
 - Polyodon folium
 - Acipenser ruthenus
 - Amia calva
 - Lepidosteus osseus
- TELEOSTS
 - MALACOPTERYGII
 - Elops saurus
 - Megalops cyprinoides
 - Albula vulpes
 - Mormyrus cashive
 - Clupea harengus
 - Engraulis encrasicolus
 - Osmerus eperlanus
 - OSTARIOPHYSI
 - Erythrinus unitaeniatus
 - Cyprinus auratus
 - Blicca björkna
 - Leuciscus rutilus
 - Scardinius erythrophthalmus
 - Idus idus
 - Arius spec.
 - Malapterurus electricus

SYMBRANCHII

*Symbranchus marmoratus**Monopterus javanensis*

APODES

Anguilla vulgaris

HAPLOMI

Esox lucius

CATOSTEOMI

*Gasterosteus aculeatus**Spinachia spinachia**Syngnathus acus*

PERSECOCES

*Scomber scomber**Thynnus alalunga**Belone belone**Exocoetus evolans**Ammodytes lanceolatus**Mugil chelo**Ophiocephalus spec.*

ANACANTHINI

Motella mustela

ACANTHOPTERYGII

*Perca fluviatilis**Osphromenus spec.**Pleuronectes limanda**Rhombus maximus**Solea vulgaris**Gobius minutus**Cyclopterus lumpus**Trachinus draco**Zoarces viviparus*

PLEGTOGNATHI

Tetrodon spec.

DIPNOANS

Ceratodus forsteri

The cord of *Amphioxus*, the lowest vertebrate, is so primitive in character that a comparison of its parts with those of higher members of the phylum is not altogether possible. On cross section it is triangular in shape, with a concave base. The gray matter is massed around the central canal, and does not show any indication of anterior or posterior horn formations (cf. KAPPERS, 1920).

In *cyclostomes* the cord shows a higher development than in *Amphioxus*. It is flattened or ribbon-shaped. The gray matter extends laterally as a wing-like expansion on either side of the central canal. There is, thus, on each side but one mass of gray matter, so that the anterior and posterior horns of higher vertebrates are not marked out, but are combined in the undivided mass. Here, as in *Amphioxus*, owing to the absence of real posterior horns, conditions such as we have in the higher forms do not exist.

In *gnathostomes* there are certain broad general features which allow comparisons of its members to be made, notwithstanding great differences in the degree of development. The cord is rounded or oval, and the gray matter on either side shows anterior and posterior horns.

Among the *selachians*, the lowest fishes, we find in sharks an arrangement of the gray matter as shown in figs. 1 and 2.

In *Hexanchus griseus* (fig. 1) the well developed anterior horns run ventrally and laterally, in *Acanthias vulgaris* (fig. 2) chiefly laterally. The posterior horns pass backwards and laterally from an undivided mass of gray matter situated behind the central canal, which I shall call the *corpus commune posterius*, to within a short distance of the surface of the cord.

While the general shape of the posterior horns in these two sharks is practically similar, namely somewhat cone-shaped with the blunt apex separated from the surface by a narrow band of fibres, the arrangement of the details is slightly different. In both forms a small triangular band of fibres separates the diverging posterior horns from each other. This mass of fibres consists of the posterior funiculi of these animals, which are very small in comparison with those of mammals (BROUWER, 1915),

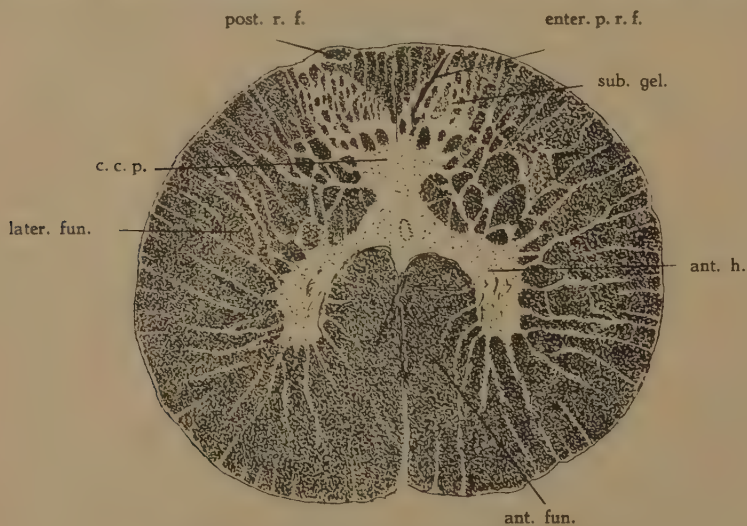


Fig. 1. Transverse section near the cranial end of the spinal cord of *Hexanchus griseus* $\times 17$.

ABBREVIATIONS FOR ALL FIGURES.

ant. fun., anterior funiculus.	interm. area, intermediate area.
ant. h., anterior horn.	later. fun., lateral funiculus.
ant. r. f., anterior root fibres.	Mauth. f., Mauthner's fibre.
c.c., central canal.	post. fun., posterior funiculus.
c.c.p., corpus commune posterius.	post. r. f., posterior root fibres.
enter. p. r. f., entering posterior root fibres.	sub. gel., substantia gelatinosa.
fasc. med., fasciculus medianus.	

and are not of the same nature. The columns of GOLL and BURDACH are either very small or are absent. The bulk of the posterior funiculi is formed

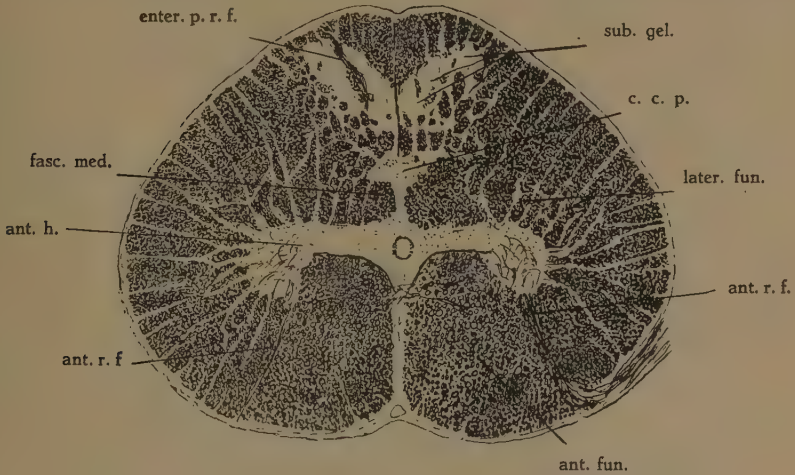


Fig. 2. Transverse section near the cranial end of the spinal cord of *Acanthias vulgaris* $\times 25$.

by descending axones of dorsal funicular cells (v. LENHOSSÉK, 1895), such as are still represented in man in the cornu-commisural bundle (cf. KAPPERS, 1920).

In *Hexanchus griseus* the most dorsal parts of both posterior horns are more separated, while the connection with the corpus commune posterius is broader than in *Acanthias vulgaris* (cf. figs. 1 and 2). In *Hexanchus* the corpus commune posterius is broad and prominent, and attached to the anterior horns by a wide stalk. In *Acanthias* this body is prominent behind, where it is continuous with the posterior horns. Ventrally it narrows until its connection with the anterior horns is drawn out into a slender stalk, on either side of which runs the fasciculus medianus, descending from the vestibular region of the oblongata. *Acanthias*, therefore, has an appearance as if the anterior and posterior horn regions were more pulled apart than in *Hexanchus*.

This is even more conspicuous in the case of *Spinax niger* where the stalk of connection is very much elongated.

The posterior roots enter the cord near the apex of the posterior horn, and run for some distance cranially, lying between the tip of the horn and the surface (the region corresponding to Lissauer's zone in higher vertebrates), where they are easily recognized because of their coarse appearance. They remain as a quite distinct bundle here, especially in *Hexanchus* (fig. 1). In *Acanthias* the root fibres spread out in a somewhat semi-lunar manner. They are more intimately mixed with the fibres at the

apex of the posterior horn. Further cranially, these root fibres pass ventrally through the substance of the horn towards its base. I have traced fine fibres from the posterior roots to the corpus commune posterius in *Spinax niger* and to the corresponding area in the ray *Raja clavata*, this animal being especially favourable because of the root entering through the lateral part of the horn, and of the fan-like expansion of the fibres towards their terminations so that the ventral expansion to the intermediate area is easy to follow (fig. 3). The coarse fibres could be traced to the longitudinal bundles which traverse the posterior horn where the greater part of them enter as ascending and descending fibres. These ascending and descending bundles are very small in comparison with the posterior columns of higher vertebrates (BROUWER, 1915).

In *Hexanchus* these intra-cornual longitudinal bundles are more numerous than in *Acanthias*. The posterior horns are completely broken up by small bundles, and at the base of the horn, at its junction with the corpus commune posterius, are a few larger ones: the latter are also well marked in *Acanthias*. The gray matter is continuous around the fibres as connecting strands, and on closer examination shows the characteristics of *substantia gelatinosa*. The entire gray matter of these horns is of this character.

In *Acanthias* the fibre-bundles are more compact and less numerous, so that the gray matter is collected into larger masses, and the gelatinous nature of the substance is easier to recognize, acquiring a greater similarity to the *substantia gelatinosa* of mammals. It is present in much larger quantities than in *Hexanchus griseus* or *Spinax niger*.

As far as could be ascertained there is no variation in amount at the point of entrance of the root fibres, but it approaches nearer the surface, probably on account of neurobiotactic influences. This is especially noticeable in *Acanthias vulgaris*.

It is clear, therefore, that these posterior horns differ in character from those of higher vertebrates, where the *substantia gelatinosa* forms merely a cap for the body of the posterior horn proper. We are led to the conclusion that the body of the posterior horn, so large in mammals, is very small in sharks, and chiefly represented in the undivided intermediate mass of gray matter, the corpus commune posterius. On tracing this intermediate mass of gray matter cranially it is found to divide, in the lower region of the medulla oblongata, into two parts, which become separated from each other by the opening out of the central canal to form the fourth ventricle. Each subdivision becomes continuous with the commissural nucleus of the vagus on its own side. This would seem to indicate a visceral association for the column, which assumption is further strengthened by the fact that in several species (*Spinax niger*, *Chimaera monstrosa*, *Raja clavata*) fine fibres from the posterior roots could be traced into it.

The fibres at the apex of the posterior horns do not show the characteristics of those of Lissauer's marginal tract as described for mammals. They are coarser, more heavily myelinated, and more closely packed together.

That they are not of the same nature is probable. At any rate the posterior roots do not contribute fine medullated fibres to this region, as can be seen to occur in higher animals.



Fig. 3. Transverse section near the cranial end of the spinal cord of *Raja clavata* $\times 18$.

In the ray, *Raja clavata*, the substantia gelatinosa is well developed (fig. 3). The intermediate mass has become drawn apart into the lateral wing-like expansions which are continuous with the substantia gelatinosa on either side, so that a greater resemblance to the posterior horn of higher animals is produced, the more so, as each intermediate wing also connects with the anterior horn. The fasciculi mediani are closely approximated between this region and the anterior horns, and in consequence the connecting gray matter is reduced, as in *Acanthias vulgaris* and *Spinax niger*, to a narrow strand.

The substantia gelatinosa occupies a somewhat quadrilateral area, and is well pronounced, though broken up by groups of fibres as in lower forms. The long axis of this mass is placed transversely, and extends from the posterior septum medially to within a short distance of the cord laterally. The posterior border is slightly convex. At the posterior septum the mass comes into contact with that of the opposite side. In many places the septum is absent, and there is a structural continuity.

A wide band of fibres separates the horn from the dorsal surface of the cord. This narrows laterally where the postero-lateral angle of the gelatinous substance comes nearer the surface, and at this point the root fibres enter. These as stated above spread out fan-like in the posterior horn, the most ventral fine fibres running towards the lateral wing of the

intermediate mass, while the remainder becomes associated with the longitudinal bundles which traverse the horn.

Chimaera monstrosa, which exemplifies the condition in the *holocephalians*, resembles the sharks more closely than the rays (fig. 4). The corpus commune posterius approaches closer in type to that of *Hexanchus* than of *Acanthias*.

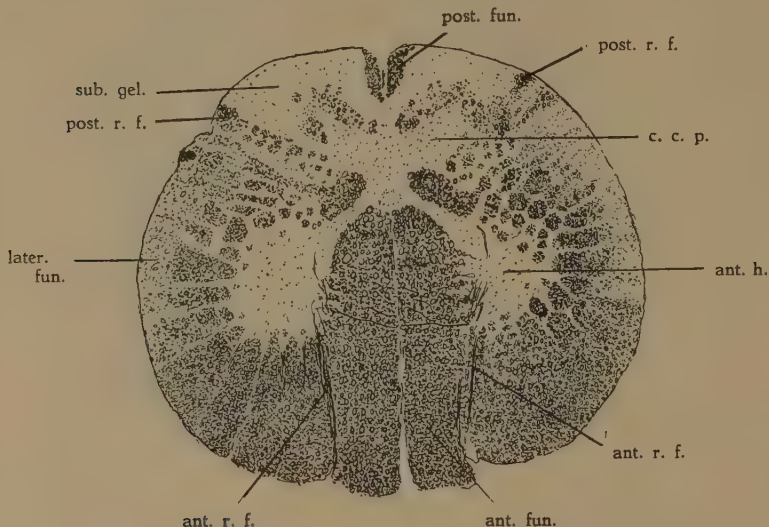


Fig. 4. Transverse section near the cranial end of the spinal cord of *Chimaera monstrosa* $\times 25$.

The limits of the area of substantia gelatinosa are somewhat hard to define owing to the slight staining of the specimen. The fibre bundles which in other species are scattered irregularly through the horn are here more compact. The posterior root fibres enter at the lateral angle of the area, and pass through the lateral part of the horn towards the region of the fibre bundles.

In view of the demonstration by RANSON (1911, 1913) of unmyelinated fibres in the peripheral nerves and posterior roots of mammals, and the importance he attaches to them as being the chief supply to the substantia gelatinosa, I examined a specimen of *Chimaera monstrosa* stained by Cajal's silver method to determine if similar relations exist here.

In the cat, RANSON (1913) points out that the posterior root on entering the cord divides into two parts; a lateral, consisting mainly of unmyelinated fibres but having also a few finely myelinated, which passes through Lissauer's zone and enters and ends in the substantia gelatinosa, and a medial which enters the posterior funiculus and is distributed in the manner generally described for the posterior root.

I was unable to find a similar state of affairs in this specimen. In the Weigert-Pal preparation the cord is very poorly stained, especially laterally and dorsally, and this applies also to the posterior roots where only a few lightly stained fibres can be seen

(fig. 4). In the silver preparation these lightly stained areas take on a dark colour owing to the number of closely packed axones present. The posterior root shows a great increase in fibres and on tracing these into the cord they traverse the lateral part of the horn, remaining a compact bundle until they reach the fibre bundles which run longitudinally through the base of the substantia gelatinosa, with which the majority of them becomes associated. Some fibres pass ventrally towards the corpus posterior. There is no separation into distinct myelinated and unmyelinated parts.

The *ganoids* present even greater differences among themselves in the structure of the cord than the selachians. Generally speaking, they approach more closely in development to that of higher forms, but many members of the group present features characteristic of selachians. *Acipenser ruthenus*, especially, resembles *Hexanchus* in the structure of the corpus commune posterius.

The posterior horns are somewhat quadrangular on section. The substantia gelatinosa is easily identified from the surrounding gray matter, and occupies the entire posterior projection or horn. It is in contact with the white matter along a very irregular line, especially towards the periphery where it sends expansions dorsally, thus presenting a dentated appearance. It is separated from the posterior septum by a small accumulation of fibres. Within this posterior horn the gelatinous substance has a closer relation to that of higher forms than is the case with selachians. It is massed into irregular accumulations practically devoid of myelinated fibres. Between these nuclear-like masses and in linear arrangement are bundles of myelinated fibres.

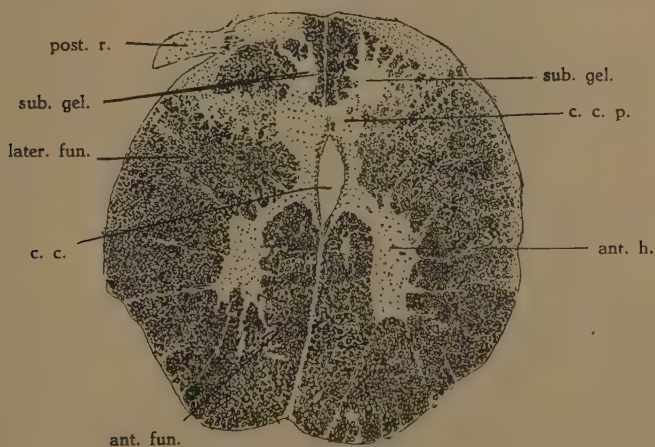


Fig. 5. Transverse section near the cranial end of the spinal cord of *Polyodon folium* $\times 90$.

Polyodon folium resembles the last mentioned very closely (fig. 5). The substantia gelatinosa is easily delimited because of its flowing together to form a single mass devoid of myelination. It is very irregular in outline

especially towards the periphery, and here also the dorsal projections are marked. It is not so abundant in *Polyodon* as in *Acipenser*. In *Amia calva* it approaches very closely in arrangement to that of the teleosts. The gray matter is arranged in a *H*-shaped manner as in higher forms (fig. 6), so that the corpus commune posterius of lower forms has disappeared as such, and merges with the surrounding gray matter. The posterior horns are very large pear-shaped structures, with the wide end directed dorsally and slightly laterally, and the narrow end or stem continuous with the anterior horns on either side of the central canal. As in the types already described they consist of gelatinous substance, merely a small area at the central end being of different structure, so that the substance in this animal reaches very great development. Medially a triangular mass of fibres, with the base directed ventrally, separates the horn from the posterior septum. The narrow apex is continuous with the fibres which cover the horns dorsally. The great massing of substantia gelatinosa within the horn produces a bulging on the surface and causes a distinct posterior fissure. Laterally a depression is formed between this bulging mass and the ventrolateral part of the cord, from the bottom of which a small septum projects inwards.

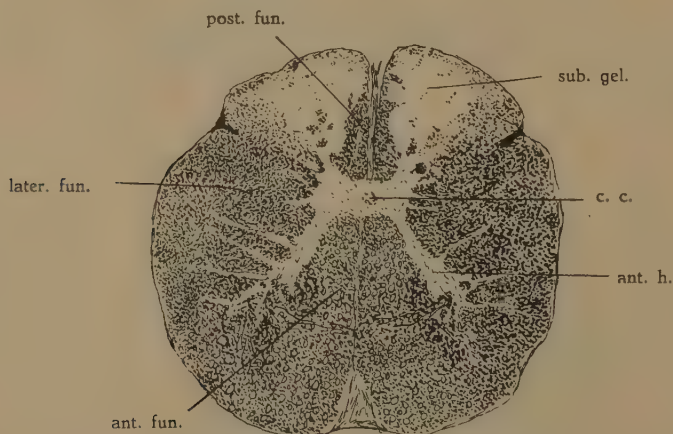


Fig. 6. Transverse section near the cranial end of the spinal cord of *Amia calva* $\times 37$.

The arrangement of the substantia gelatinosa within the horns, as in many teleosts, is in small masses, which may be partly or completely surrounded by myelinated fibres, the whole arrangement presenting the appearance of an accumulation of several "nuclei". The fibres may surround these in a concentric manner, and in many cases, especially in certain teleosts, a hilum-like arrangement is present through which fibres can be seen to pass. In other cases the substantia gelatinosa is folded around a

central core of fibres ("internal cortical lamination" of KAPPERS, 1914). In this species masses are indicated as forming clumps but are not surrounded by fibres.

The posterior roots enter the cord near the lateral edge of the posterior horns, where they divide into ascending and descending branches, and become indistinguishable from the covering fibres.

In two other species of this group examined, *Calamoichthys calabaricus* and *Lepidosteus osseus*, the substantia gelatinosa is present in medium quantity and development. *Lepidosteus* deserves special mention because of its resemblance to *Spinax niger* and *Acanthias vulgaris* in the arrangement of the corpus commune posterius, its attachment to the anterior horns being reduced to a narrow strip.

The great class, *teleosts* including, as it does, animals of such varied appearances, sizes and modes of life, presents many differences in the structure of the cords, some of which, indeed are so marked as scarcely to allow of a typical description (cf. *Albula vulpes* and *Osmerus eperlanus*). Looked at from the point of view of the presence or absence of gelatinous substance and its relations to the posterior horns such a typical description will perhaps suffice.

The teleosts are sometimes described in common with the ganoids under the heading Teleostomi, but, owing to the primitiveness in arrangement of the substantia gelatinosa in most members of the ganoids and the general resemblance to sharks, I have described them under separate headings.

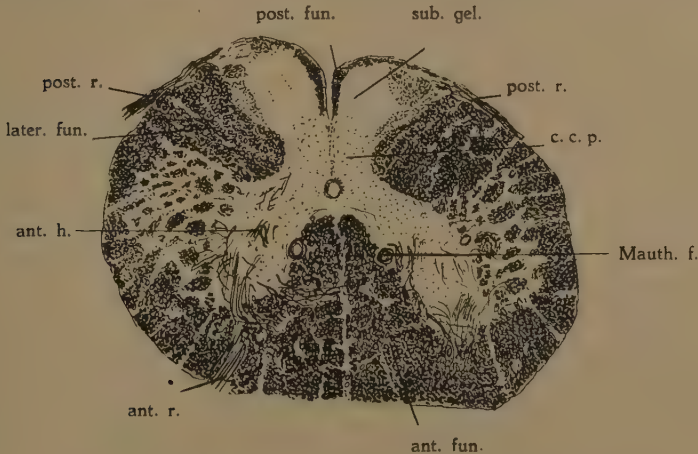


Fig. 7. Transverse section near the cranial end of the spinal cord of *Esox lucius* $\times 76$.

The teleost cord as represented by *Esox lucius* is shown in fig. 7. The gray matter has not reached the typical H-shaped arrangement seen in higher animals. In fact in regard to this character it appears more

rudimentary than *Amia calva*. The anterior horns are (as in still lower forms) separate structures, though much broken up at their ends. The dorsal region of the gray matter is made up of two oval masses (the posterior horns) united ventrally by a single mass of gray matter (the intermediate area or *corpus commune posterius*). The latter area in many cases shows an indication of division by means of a septum, represented in some places by a few indifferent cells. The *corpus commune posterius* is continuous, around the central canal, with the anterior horns.

The posterior horns diverge slightly from each other. They are covered medially by a narrow layer of myelinated fibres which is continuous round the posterior surface to the point of entry of the posterior roots. Laterally the horn is ill defined, being broken up by scattered coarse and fine fibres. It consists chiefly of gelatinous substance which is arranged in one large mass traversed here and there by fibres, coarse and fine. The posterior roots approach the cord laterally and run dorsally to the lateral angle of the posterior horn, where the greater part of the fibres continue towards the posterior funiculus; a small part, however, enters lateral to the *substantia gelatinosa* (cf. HERRICK, 1907; KAPPERS, 1920; and VAN DER HORST, 1927).

In many teleosts the arrangement of the gelatinous substance is not so simple as in *Esox lucius*. VAN DER HORST (1927) in describing this area in *Albula* says "Here the nucleus exhibits the peculiarity that it does not form a more or less compact mass as is usually the case in teleosts, but has the form of a rather thin curved lamella. Thus, it assumes a form similar to the lower olive and other, especially sensory, areas that enlarge their surface by making folds."

This curving of the mass and even isolation of parts by fibre masses occurs in many teleosts. In *Erythrinus unitaeniatus* the condition is well marked. In *Osphromenus* the isolated masses are partly or completely surrounded by fibres, many of which run circularly.

These foldings occur especially in animals in which the substance is well developed. The phenomenon also occurs amongst the mammals, especially the ungulates.

It is worthy of note that in teleosts as in lower fishes, the gelatinous substance practically fills the posterior horns. The body of the horn in mammals, therefore, in so far as it is present in fishes is very small, and seems to be represented only in the *corpus commune posterius*.

The relation between these parts in fishes and mammals demonstrates the great preponderance of *substantia gelatinosa* in the lower forms. *Albula vulpes* is a particularly good example of this relation, as here it reaches a development not approached by any other species examined, while the *corpus commune posterius* is reduced to a small area dorsal to the central canal.

Whereas part of the body of the posterior horn in mammals is probably represented in this undivided mass in fishes, still this part is very small.

This probably has to do with the small amount of projection fibres to the cerebellum and mesencephalon that arise in posterior horn cells. To this may be added that the epicritic (HEAD, 1905) or gnostic (KAPPERS, 1920) sense, that in mammals is connected with the posterior horns by collaterals of the posterior funiculi, is poorly developed in fishes.



Fig. 8. Transverse section near the cranial end of the spinal cord of *Osmerus eperlanus* $\times 76$.

As a contrast to *Esox lucius* I figure the cord of *Osmerus eperlanus* (fig. 8).

The substantia gelatinosa is easy to recognize but is poorly developed, and separated from the surface of the cord by a wide band of fibres.

The posterior roots can be seen passing to it, and in the region of the posterior horns separate into dorsal and ventral divisions which enfold the gelatinous substance. The horns themselves are not well formed. They lie on either side of the posterior septum, and are free only in the apical regions. The corpus commune posterius is very conspicuous and has a quadrilateral outline.

Regarding the degree of development in the other teleosts I may say that a reliable standard of comparison is difficult to fix owing to the differences in size and general relations in some of these cords. SANO (1909) recognized the same difficulty in mammals, where he compiled tables of measurements of the area of transverse section of the cord, the entire gray matter, the posterior horns, and the substantia gelatinosa, and worked out the interrelations of these several parts. It is doubtful if even this is complete without an examination of the constituents of the posterior roots, and the skin areas they supply.

Albula vulpes is remarkable for the very great development of its substantia gelatinosa, and it is noteworthy that some form of cutaneous

sensibility seems to be especially developed, as appears from the fact that a large cutaneous branch of the facial nerve occurs in this fish (VAN DER HORST, 1927). *Albula* is the only teleost in which such a branch has been so far described. The presence may add to the great development of the substantia gelatinosa in the cervical cord of this animal. Perhaps in the sensory spinal roots a similar increase of analogous fibres occurs that may be responsible for the strong development of this substance throughout the cord.

After *Albula*, and somewhat in the following order with regard to development of the substantia gelatinosa come *Mormyrus cashive*, *Osphromenus spec.*, *Pleuronectes limanda*, *Mugil chelo*, *Gobius minutus*, *Ophiocephalus spec.*, *Perca fluviatilis*, *Esox lucius*, *Megalops cyprinoides*. All these show well-marked gelatinous substance. Those showing least development are *Zoarcus viviparus*, *Motella mustela*, *Idus idus*, *Osmerus eperlanus*, *Monopterus javanensis*, and *Malapterurus electricus*, while the general body may be described as intermediate in development.

A perusal of the list will show that this order is very irregular in regard to the classification given.

Most of my observations were made on sections of the cranial end of the spinal cords. In some teleosts a larger part of the cord was available, and in *Albula vulpes* I had an opportunity of studying the cord in its entire length. At the cranial end, where the descending fibres of the trigeminal, facial, and vagus nerves are still present, the substantia gelatinosa is very massive, occupying a little less than half the entire section (cf. also VAN DER HORST, 1927). It presents here two or more folds. Below the point of disappearance of trigeminal, facial, and vagal fibres it decreases considerably in size, and there is an accompanying simplification in the folding. Traced caudally, there is a gradual reduction of the gelatinous substance until the tail region is reached, where again a slight increase occurs. This is in accordance with what is generally known concerning the sensibility of the cord of fishes viz., that the head region is the most sensitive, after it the tail, the body being the least specialized. The cord of fishes is not complicated, as in higher forms, by cervical or lumbar enlargements. Notwithstanding the reduction, the development in the tail region is still considerable (fig. 9), exceeding in fact that of the cranial region of most forms. The arrangement in this region is, however, relatively simple, merely a single fold around a core of slightly myelinated fibers. The root fibres behave as in *Esox lucius*, dividing into two parts, the larger running dorsal and the smaller lateral to the horn. The dorsal passes round the substantia gelatinosa and some of its fibres reach the posterior funiculus which, in the interval between the roots, is an isolated bundle.

Finally in fig. 10 I give the condition in the *Dipnoi* as represented by *Ceratodus forsteri*. The cord appears fairly high in type though it still presents characteristics which betray its lowly connections. The gray

matter, however, shows a more typical H-shaped arrangement than in any other fish. The medial part of the corpus commune posterius is reduced in the region of the dorsal gray commissure. Its lateral parts are probably incorporated in the posterior horns which are very simply constituted. They



Fig. 9. Transverse section near the caudal end of the spinal cord of *Albula vulpes* $\times 51$.

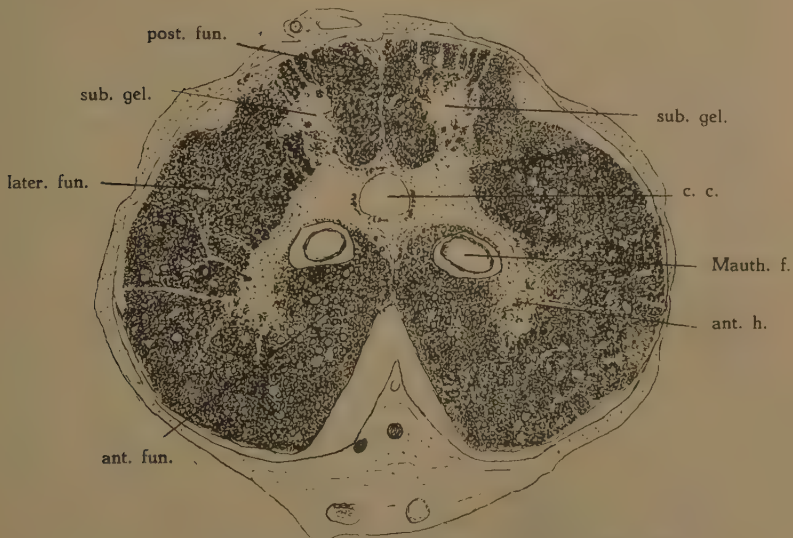


Fig. 10. Transverse section near the cranial end of the spinal cord of *Ceratodus forsteri* $\times 33$.

consist of an irregular mass of gelatinous substance on either side, which is almost isolated from the rest of the gray matter by a layer of medullated fibres situated at the neck.

The posterior funiculus is more massive than in teleosts, and reminds us of the condition in frogs (cf. KAPPERS, 1920, fig. 75). The horns are separated from the surface by a fairly wide band of fibres. Though the development of the substantia gelatinosa is not as extensive here as in most teleosts, it is still the ground-work of the posterior horns.

RESUMÉ.

A study of the posterior horn region of the cord of lower vertebrates gives us an idea of the principles on which that of higher forms is evolved. Beginning with *Amphioxus*, we find a very rudimentary condition, in which horn projections are not even indicated. In *cyclostomes* a single mass is present on either side.

The *fishes* show the beginning of the condition found in higher forms. The anterior horns are definitely indicated, though not sharply defined, and are usually broken up at their ends. The posterior horns are rudimentary projections from a single mass of gray matter which lies dorsal to the central canal. This body I have designated the *corpus commune posterius*. It is present throughout the different groups of fishes, though in various degrees of development. In *Raja clavata*, *Amia calva*, and *Ceratodus forsteri* it is much reduced, and replaced by bilateral structures, in which respect they resemble the higher forms. Still the posterior horns differ essentially in structure from that described for man. Whereas, in the latter, three areas may be distinguished from the centre to the periphery — body of the posterior horn, substantia gelatinosa Rolandi, marginal zone of Lissauer — the posterior horns of fishes mainly consist of substantia gelatinosa. The bodies of the horns of higher forms are (in part at least) represented in the *corpus commune posterius*. That this has chiefly a visceral function is probable from the facts (1) that cranially it becomes continuous with the commissural nucleus of the vagus in the medulla oblongata, and (2) that fine medullated fibres from the posterior roots can be traced to it.

A comparison of the relations between the body of the posterior horns and the substantia gelatinosa in mammals, and of the corresponding areas in fishes demonstrates the small size of the body of the horn and the great size of the gelatinous substance in the latter. In *Albula vulpes* this is especially striking. In the cranial end of the cord it almost fills the posterior horns, and occupies nearly half the total area of cross section. While according to SANO's tables, on the same level in man it occupies half the posterior horn, and about one-thirty sixth of the entire cross section.

Another difference between the posterior horns of fishes and mammals is that in the latter they are pushed far apart by the accumulation of fibres

to form the columns of GOLL and BURDACH in the posterior funiculi. In the former where these columns are small the horns lie close together; where the fibres are absent they are separated merely by the posterior septum, and even this may be wanting, so that they are structurally continuous.

What is the function of this nucleus, so prominent in lower forms but which loses in relative size in the higher animals? SANO (1909) concluded it could not have a wholly cutaneous sensory function because he found it best developed in mammals which were not at the top of the scale of sensitivity. He suggested a sympathetic function, but found little support, even in his own work for such an assumption.

In fishes which present well-developed *substantia gelatinosa* there is usually evidence of great cutaneous stimulation (*Albula*). Amongst those of poor development the reverse seems to be the case.

These results appear to support the view of RANSON (1915) that this substance is related to primitive sensation (protopathic of HEAD, 1905; vital of KAPPERS, 1920). As vital sensation is probably the only kind in fishes, we should expect variations in the nucleus in the same directions as skin sensibility. I intend, however, to discuss this subject more fully in a subsequent contribution.

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Comparative Physiology. — *About the influence of the nerve-centres on the antagonistic neuro-muscular-systems in the periphery of the cray-fish.* By J. SEGAAAR. (Communicated by Prof. H. J. JORDAN.)

(Communicated at the meeting of September 29, 1928).

The physiological examination¹⁾ of which the information mentioned below gives some results, finds its starting-point in two groups of experiments which have been made on the same species of animals or on one which is very much related to it.

I. *The inhibition of the isolated cray-fish claw.* To these and the other extremities applies, as has been shown by RICHET (1) and afterwards by BIEDERMANN (2), that strong stimulations cause bending, whereas weaker ones cause stretching. The antagonists of the claw-muscles answer these stimulations respectively with shutting and opening. Histologically it has become a fact by the investigation of BIEDERMANN (2) for *Astacus* and by the one of MANGOLD (3) for other Arthropoda, that to each muscle-fibre run two axons. By reason of this histological datum and of the fact, that with strong currents the claw shuts itself and the opener-muscle relaxes at the same time BIEDERMANN set up the hypothesis, that one axon can only work exciting, the other only inhibiting.

In 1914 appeared the excellent work of P. HOFFMANN (4), who analysed further the antagonistic nerves. These experiments have been thoroughly repeated and enlarged in our laboratory by REITSMA and DU BUY (5). They could affirm the examination of HOFFMANN and accept with him the BIEDERMANN hypothesis as proved.

As for the histology it is of importance to us here 1^o. that both axons of the opener-muscle (there are altogether only two axons running to this muscle) can be quite continued up to the claw-ganglion. They pass into two nerves, which are to be observed macroscopically and which represent themselves as a thin and a thicker system; 2^o. that all anastomoses in the periphery are wanting.

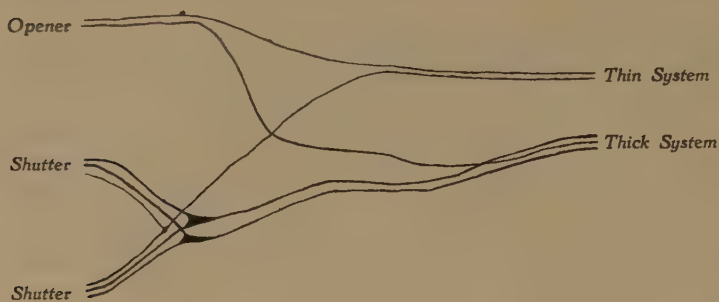
HOFFMANN gives the following scheme, which I myself had the opportunity to test (p. 856).

Through this classification we are able to examine individually both axons e.g. of the opener-muscle.

For this purpose only one of the nerves is cut through and the other axon can then be examined on its inhibitory or excitatory properties. For the first it is self evidently necessary that the concerning muscle is in a certain tonus, so that it must be excited, if absent, by a suitable artificial stimulation.

¹⁾ Begun July 13th 1927.

With the openermuscle its excitator passes into the thin system, its inhibitor into the thick system. For the shutter this is just the other way



round. For this one the inhibitor runs into the thin system, the excitators (here 5 or 6 axons of which only two have been drawn in the scheme) into the thick system. According to H. an inhibitory axon does nothing else but inhibiting an existing excitation and an excitator can do nothing else but exciting. H. adds to it this important remark that unlike the Vertebrata where the resultant of excitation and inhibition is situated in the centre, the compensation of these two with the Arthropoda takes place in the neuro-muscular junction in the muscle. As a second contrast to the Vertebrata where inhibition means: not being excited, H. considers the inhibition with the Arthropoda as an "opposite excitation", in other words the peripheral inhibition in this group of animals would be a process sui generis.

Through H.'s examination the hypothesis of FRÖHLICH (6) does not hold good any longer, because he understood the inhibition to the analogy of peripheral phenomena in the neuro-muscular preparation of the Vertebrata as Wedensky-inhibition, that is to say that the muscle achieves less at a high frequency than at a lower as a consequence of fatigue. At the same time the view of VON UEXKÜLL and GROSS (7) falls away, who in virtue of histological investigation concluded, that a nerve-net existed in the periphery, into which the openermuscle as well as the shutter were to debouch and from where the nervous impulse was to be distributed. Opposite to this HOFFMANN puts specific inhibitory nerves (axons) in which a disturbance of balance in virtue of the peculiarity of the nerve means inhibition.

II. *Inhibition in the periphery by a central impulse.* Experiments about the influence of the centre on the periphery have been made by JORDAN (8) on *Cancer pagurus* and *Astacus fluviatilis*. JORDAN thinks there, that excitation and inhibition of the antagonists in the extremities just as in the periphery itself can be imitated by an electric stimulation of the centre. The remarkable fact in this is however, that with respect to the strength of

the stimulation quite reversed results are obtained ; when JORDAN stimulated the brains or the connectives of the esophagus, he caused : with weak currents : flexion (resp. shutting) and with strong ones : tension (resp. opening).

In accordance with the direct stimulation of the claw, also with stimulation of the brains, the excitation of a muscle is attended with the inhibition of its antagonist. Further JORDAN could prove that both ways of stimulation can interfere with each other in an inhibitory way, so that the effect of a peripheral stimulation e.g. flexion, can be neutralized by a simultaneous stimulation of the brains, while after interruption of the central and continuation of the peripheral stimulation, flexion immediately begins again.

As is known, these animals after onesided extirpation of the cerebral ganglion perform manege-movements, with which the extirpated half is always turned to the outside. It was just these phenomena which brought JORDAN to the above-mentioned experiments. Without my going into further details, let it be mentioned, that JORDAN was able to imitate the influence of the missing brain-half through stimulation with a certain strength of the connective got free after onesided extirpation in such a way, that he could bring back the animals to normal locomotion again, or even to a circular motion in opposite sense. By regulating the quantity of these one-sided connective-impulses JORDAN could "direct" the animals to the left or to the right, so it determines, whether the periphery is influenced in the sense of inhibition or excitation.

Herewith a provisionally satisfying explanation was given of the manege-movements and was shown at the same time, that by cooperation of periphery ¹⁾ and centre coordinated walking-movements come about.

A question which can be put in the first place in connection with JORDAN's investigation is : Whence the phenomenon that e.g. *strong cerebral innervation gives the very opposite result of strong peripheral stimulations* ?

The solution to this question was to be found in anatomical or functional direction or in both. It might e.g. be possible that strong cerebral stimulations, instead of being able to act on the excitator of the shutter, are changed over on its inhibitor. Physiologically it is to be found in a change of strength of the nervous impulse, so that e.g. the strong cerebral stimulations in the claw ganglion are shifted to weak ones and otherwise weak stimulations to strong ones. The last point of view, however, at close observation meets with this difficulty that a peripheral opening stimulation gives by far a less intensive reaction, and also one, which lingers on for a shorter time than a central stimulation with qualitatively the same effect, and the same thing, but then predominantly to the periphery, is applicable to closing-stimulations.

By the side of this, the first-mentioned possibility would be a hypothetical expedient, which was to find its affirmation in a histological examination.

¹⁾ Here the claw ganglion.

The histology of the thoracal nerve-cord (DROOGLEVER FORTUYN (9)) is still unknown, however, and yields many difficulties to the examination.

Another question, namely with regard to the manege-movement, is, whether the latter can entirely be explained from the domination of the flexors of the abnormal side over those of the normal one; in other words: is the one last-mentioned, really normal? With *Cancer pagurus* this may be likely at first sight, a manege-crab gives besides the non-equivalence of the two symmetrical halves also the impression that the whole animal even at rest is prepared for this walk. So this would come to the crossing of tracks and the crossed reflexes contingent upon it, which BETHE (10) denies for the Crustaceae. For these, as well as for other questions I must refer, however, to a publication, which is to come out later on.

With the help of HOFFMANN's excellent analysis I have tried, now to come to a further solution as to the question formulized on page 857. This question may be modified as follows: *What kind of influence has cerebral stimulation on the four isolated neuro-muscular-systems? Is a definite concatenation of the neurons present, or is there an alteration in the excitation-state in the claw-ganglion?*

The methodics for the examination are the following:

1st *mechanograms*: The object is put on a register-apparatus, which is to be explained more in details in a following publication and two writers of which take down the opening and the shutting (resp. their inhibition of the left and the right claw on a kymographion. One of the two claws is kept in a normal condition; it receives only cerebral stimulations, through which (approximately on account of contingent difference of threshold between left and right) we are able to state what the unimpaired claw will do in case of cerebral stimulation. The antagonistic systems of the other claw are isolated and these are either all centrally or, besides this also peripherally stimulated by putting the electrodes of a Ruhmkorff in the basis of the claw or in the 2nd limb. The isolation occurs as follows: After the tegument of the arthrosis has been cut through between the second and third limb (Carpo-Meropodiet) the thin or the thick nerve system is cut through at that place and besides this also the opener- or the shutter-tendon, which are attached to the movable claw-ast (Dackylopodiet).

By this 4 possibilities come into existence:

Thick system + shutter tendon cut through gives isolated openeraxon I									
Thin	+	"	"	"	"	"	"	"	II
Thick	+	opener	"	"	"	"	"	"	shutteraxon II
Thin	+	"	"	"	"	"	"	"	shutteraxons I

In these mechanograms p (= tendon) and sp. (= muscle) are used promiscuously.

Those marked with I are the excitators in HOFFMANN's experiments and those with II the inhibitors. This nomenclature cannot be maintained, however.

2nd *Electrograms*: It goes without saying that the same diagrams of isolation were applied to these. Only the proximale end of the muscle was cut through instead of a tendon, to avoid all action-currents in it. For the method of leading of the action-currents, together with the regulation in order to prevent induction, superfluity of current, and the like, I refer to my publication.

All stimulations occur by means of faradization.

Results: *Shutteraxons I*. (Fig. 1, 2, 3, 4 and 5.) When the threshold-

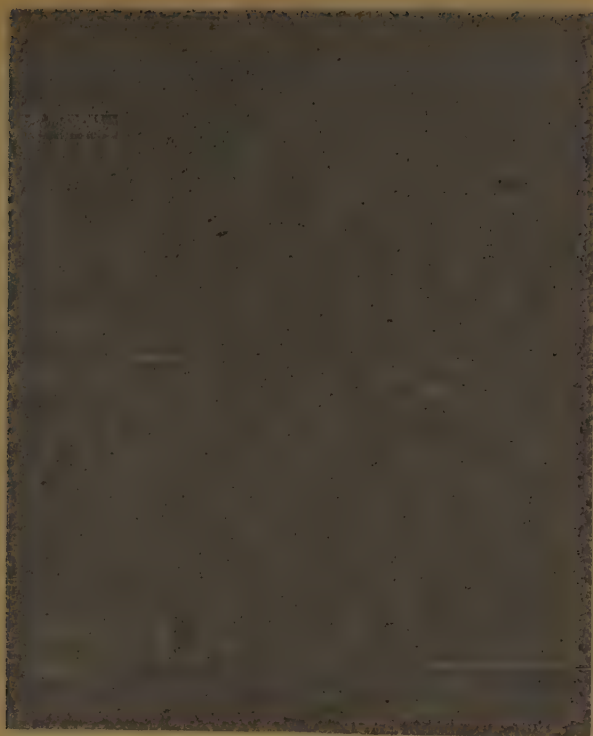


Fig. 1. Shutteraxons I, examined for weak to strong cerebral stimuli. R, norm. = right claw is left normal. C.p. = cerebral stimulation. L, du's, f. 2nd = f. 1st = left claw thin system and open muscle cut through. With R.A. = 11 (stimulation 11) the left claw closes submaximally; with R.A. = 10 $\frac{1}{2}$ maximally; with R.A. = 10 less again and this is also the point at which R. begins to open, and it opens a great deal more as the stimulus increases. The left claw, however, does not close any more. R.A. = 9 $\frac{1}{2}$, so is a strong stimulus here. The velocity of the drum is in all experiments 1 cm = 4 sec.

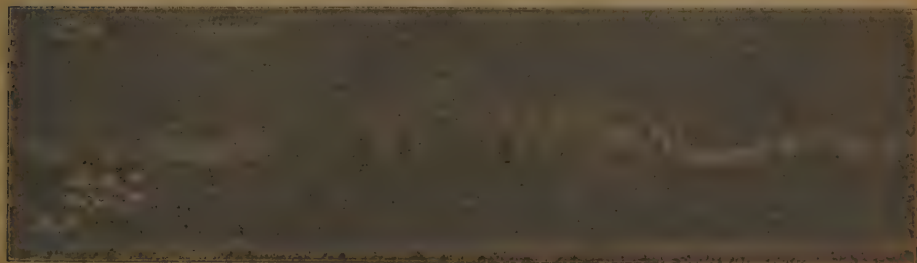


Fig. 2. Shutteraxons I for weak cerebral stimuli. A peripheral current of 100 mA, which increases in frequency by a weak cerebral stimulus. The velocity of the drum = 0.4 sec. Sensitivity, 1/2 cm = 1 mV.

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Thin	..	+	II
Thick	..	+	opener	shutteraxon II
Thin	..	+	shutteraxons I

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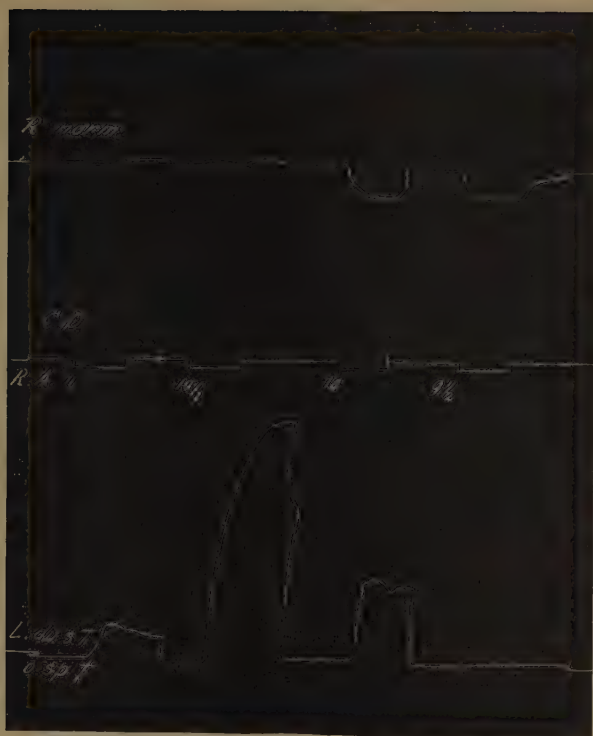


Fig. 1. *Shutteraxons I*, examined for weak to strong cerebral stimuli. *R. norm.* = right claw is left normal. *C. p.* = cerebral stimulation. *L. du s. f* and *o. sp. f* = left claw thin system and openmuscle cut through. With *R. A.* = 11 (coil-distance 11): the left claw closes submaximally; with *R. A.* = $10\frac{1}{2}$: maximally; *R. A.* = 10: less again and this is also the point, at which *R.* begins to open, and at which it ever opens more as the stimulus increases. The left claw, however, does not close any more. *R. A.* = $9\frac{1}{2}$: so is a strong stimulus here. The velocity of the drum is in all experiments: 1 cm = 4 secs.



Fig. 2. *Shutteraxons I* for weak cerebral stimuli. A peripheral stimulus gives action-currents, which increase in frequency by a weak cerebral stimulation. In all electrograms 1 cm = 0.44 sec. Sensitivity: $1\frac{1}{2}$ cm = 1 m.V.

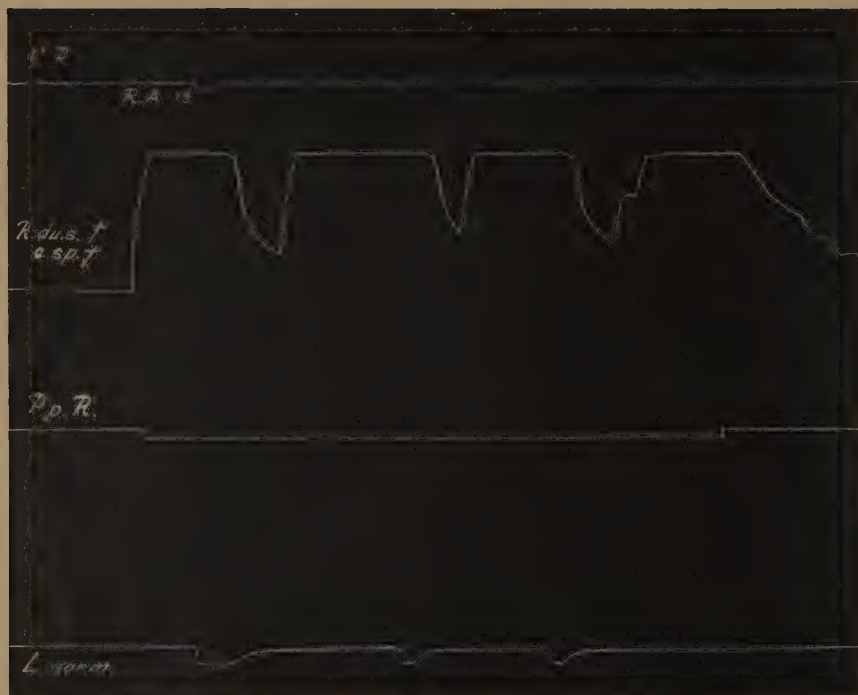


Fig. 3. *Shutteraxons I* for strong cerebral stimuli. *P.p.R.* = peripheral stimulation of right claw. By this it is closed, which is inhibited by cerebral stimulation, while at the same time the left claw opens. The threshold is lower here than in fig. 1; *R.A.*: 13 is already a strong stimulus. Attention is drawn to the moment of *C.p.* and the beginning of the inhibition and the aftereffect of it.



Fig. 4. *Shutteraxons I* for strong cerebral stimuli. The adductor is brought to contraction by reflexory stimulation by bringing a glass staff between the asts of the claw. This contraction is inhibited by *C.p.*, after a distinct "twitch" has first passed. Distinct after-effect of inhibition. 1 m.V. = $1\frac{1}{2}$ cm.

value for cerebral stimulation is attained, then these weak currents cause shutting, which at first increases proportionally to the strength of the stimulation, but never attains the strength of peripheral stimulation. If we

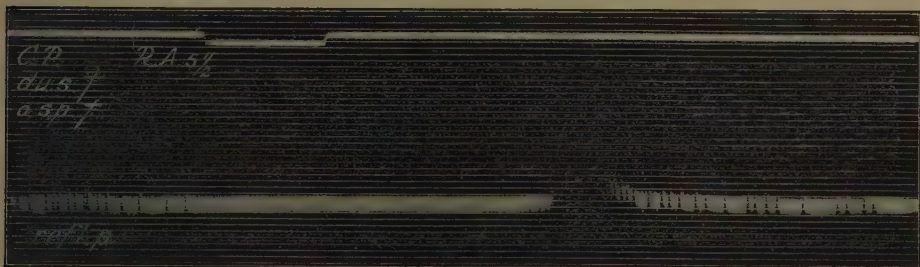


Fig. 5. *Shutteraxons I*. C.p. has been taken here even stronger. A "twitch" fails, but after-effect of inhibition and "rebound contraction" is distinct. 1 m.V. = $1\frac{1}{2}$ cm.

increase the strength still more, then the *response decreases again*. After this, two phenomena may appear: 1st The response is entirely reduced to the zero-line. 2nd In a number of cases, mostly with tiredness, the muscle answers the stimulation with a simple "twitch", but never with a lasting tetanus.

The question arises now, whether these stronger stimulations are not conducted by the nerve. This is really the case, but in another way than we should expect. This is evident when we give the muscle a certain tone or when the latter is in that condition by nature. With the above-mentioned stimulation-strength and with a higher one, appears then that the cerebral stimulation does attain the muscle or at least the nerve-ending, but does not give excitation or strengthening but on the contrary inhibition of an existing muscletone, or as we saw, only makes the tone maximal by a "twitch" and then inhibits. This central influence through these axons I is most obvious when we cause peripherally a submaximal tetanus. Weak stimulations will render the latter maximal then, stronger ones will take a more or less reducing effect. So we have come to the first particularity viz.: *that this system which peripherally shows increasing contraction-height with increasing stimulation-strength, takes down from the centre first an optimum-curve of contraction-heights with increasing strength, but changes, however, into its opposite viz. inhibition, with further increase.*

The presence of a twitch with following inhibition strongly reminds of the well-known type of Wedensky-inhibition. The way, however, in which the inhibition of an existing tone reveals itself, especially the course of time between stimulation and inhibition and the striking after-effect of the inhibition, raises objections to an explanation in that direction.

Shutteraxon II: (Fig. 6 and 7.) As it is known this axon peripherally

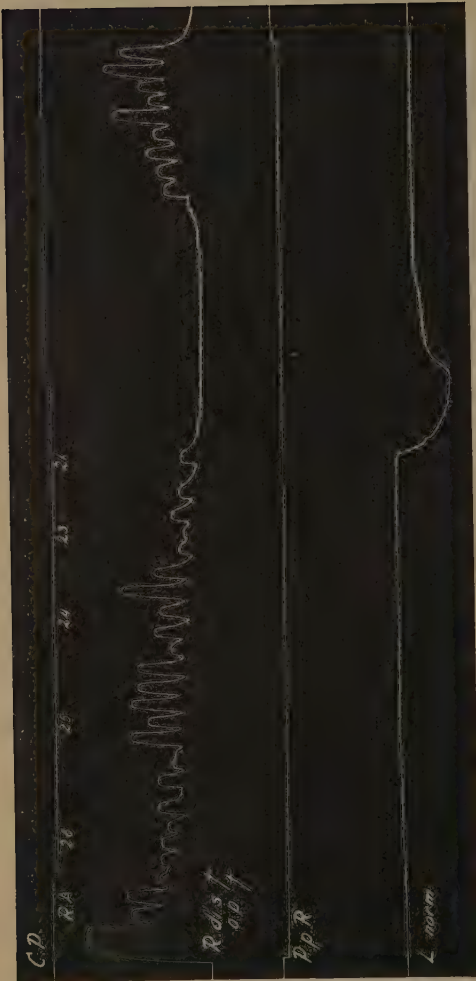


Fig. 6. *Shutteraxxon II* for weak to strong C. p.; R. d. s. t. and o. p. t. = thick system and tendon of the opener in the right claw cut through. To get a general view of the influence of various degrees of strength of stimulation, the distance between the coils was gradually diminished from R. A. 26—21.

R. A. 26: does not influence the submaximal rhythmical contractions caused by peripheral stimulation.

R. A. = 25 and 24: reinforce; R. A. 23: partial, R. A. = 21 total inhibition. On this point the normal claw opens. There is a distinct inhibitory after-action.

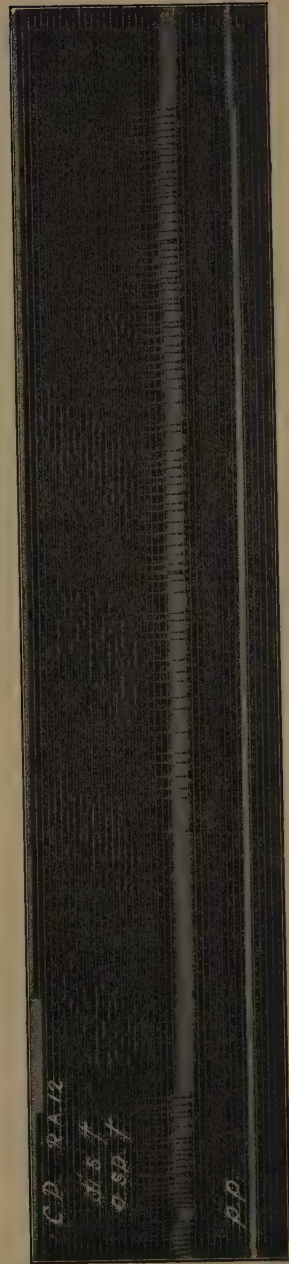


Fig. 7. *Shutteraxxon II* for strong cerebral stimulation. 1 m. V. = 1 cm.

stimulated is only known as a typical inhibitor. This is quite different with central stimulation. A peripherally made sub-maximal tone of the adductor viz. *is strengthened by weak central currents* and then this inhibitor takes an excitatory effect. With stronger central influence, this axon behaves as with weaker stimulation, peripheral. Never does this system show a "twitch". The shutter-systems I and II work together and give with strong cerebral currents the inhibition of a shutter-tone, described by JORDAN.

Opereraxon II: (Fig. 8 and 9). Also for this one the specificity of an inhibitory nerve is nullified as this is the case when it is peripherally

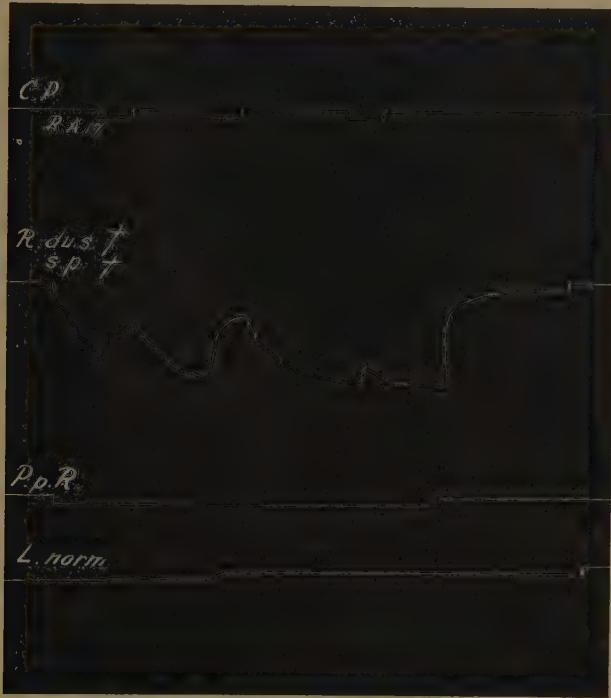


Fig. 8. (*Opereraxon II* for weak cerebral stimulation.) Thin system (*du. s.*) and shutter-tendon (*s.p.*) are cut through. Peripheral stimulation shows openertonus, which is inhibited by weak cerebr. stim. The left (normal) claw shows but little closing.

stimulated. From the centre this axon takes an inhibitory effect with weak stimulation on an existing submaximal openertonus. *With stronger stimulations on the contrary the effect is exciting.*

Opereraxon I. At first this system seemed to maintain its specificity of exciting nerve all along the line of stimulation-degrees. In a number

of cases we succeeded, however, to cause inhibition by this exciting nerve at a weak strength of current, so that the latter agrees through this with openeraxon II.

Summed up the results are :

10. Specificity of inhibitory and excitatory axons, so probable in the hypothese of BIEDERMANN and seemingly so evident in the stimulation-tests of HOFFMANN, does not exist in these antagonists. Each of the four systems can excite as well as inhibit.

20. Whereas in the peripheral stimulationexperiments the contrary-action of opener and shutter is owing to: 1. a lower threshold of the

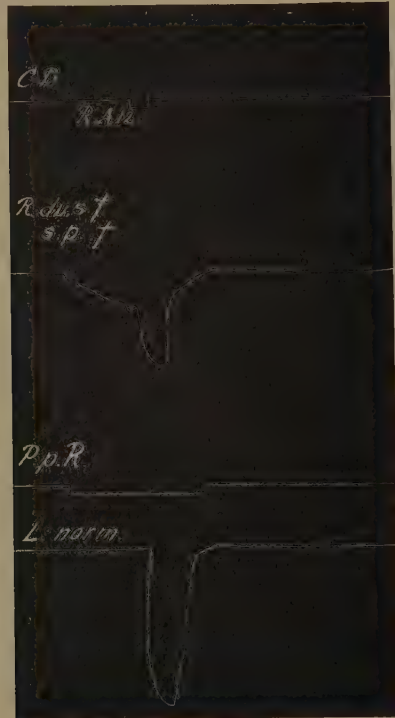


Fig. 9. (*Openeraxon II* for strong cerebral stimulation.) A submaximal opener-tonus is reinforced by a strong cerebral stimulation ($R.A. = 12$).

Accordingly the normal claw gives an opener-response.

opener-system, 2. in the domination of the shutter-system with strong currents (REITSMA and DU BUY), this is not the case centrally. Difference of threshold is not demonstrable and the result is ever a resultant of excitation and inhibition.

30. The effect of cerebral stimulation, contrary to that by peripheral

stimulation, is caused by physiological properties of ganglion-cells of the thoracic nervecord.

40. With regard to these animals, too, it holds good that inhibition is characterized by partial or total reduction of actioncurrents in the electrogram.

50. There is no evidence of the difference with the Vertebrata suggested by HOFFMANN that inhibition with the Anthropoda would mean "reversed excitation".

60. The difference with the Vertebrata that the resulting effect of inhibition and excitation does not lie in the centrum, but in the neuromuscular junction, is confirmed.

70. As with the Vertebrata typically central phenomena occur, such as "after discharge", "rebound contraction" etc. (SHERRINGTON (11)).

The answer to the question on p. 858 may be now on the basis of our experiences as follows:

10. Every form of cerebral stimulation may have an inhibitory or excitatory influence on all four nervous systems, according to its force, whereas differences of threshold for the nerves, as in the peripheral stimulation according to DU BUY, is not present here. From this it follows that a changing over as we described it above, cannot be present.

20. If there was only a question of change of force of the nervous impulse in the claw ganglion, it would be explained that inhibition is caused by the inhibitory nerves notwithstanding contrary force of stimulation, and the opposite, but not that excitation may be caused by the inhibitory nerves and inhibition by the excitatory nerves.

Discussion.

We now ask ourselves how we must picture to ourselves the relation between excitation and inhibition with our animals. The lack of specificity of a single axon for excitation and inhibition leads to supposing a parallelism with the WEDENSKY-LUCAS-ADRIAN theory for the Vertebrata, in which inhibition is a particular form of excitation, and where "an inhibitory pathway might become an excitatory at any moment, if its conductivity increased" (ADRIAN (12) pag. 415). Particularly this theory might be enlightening, where it would explain the difficulty mentioned above: the effect of the change of force of the nervous impulse, as a change in the rhythm of stimulation.

However, this theory fails to explain a number of typically central phenomena, which show themselves with the Vertebrata and also very plainly with the crayfish. Of these I mention for instance the great difference of time between stimulation and manifestation of inhibition.

Further the considerable after-effect of inhibition, which may last several seconds. It happens even that only after the cessation of the stimulation of some seconds, may the inhibition be observed and that it then produces

a long after-effect. These differences of time don't fit in the scheme which this theory gives about inhibition. Likewise the occurrence of "rebound contraction" is an objection to attributing without more ado the inhibition phenomena investigated by WEDENSKY (13) and proved by LUCAS (14) to the phenomena of the nerve-muscle preparation.

Attention is also drawn to the following fact: with the claw of *Astacus* one and the same stimulation causes contraction along one nerve, inhibition along another. Therefore it ought to be supposed that each of these nerves has a specific rhythm. Both nerves may be excited from the cerebral ganglion: the same stimulation may cause inhibition through both nerves. If there was a question of frequency here, each specific frequency of each nerve should be parallel with a definite central frequency and not with some other to produce a given effect: the same central frequency summed to the peripheral frequency of the excitatory fibre would not be able to give almost the same effect, as when added to the "specific rhythm" of the inhibitory axon of the same muscle.

In another theory of inhibition, viz. that of SHERRINGTON (15) all attention is given to the central processes and it is pointed out that the central inhibition should be considered rather a process *sui generis* than a particular form of excitation. On p. 529 S. says that inhibition can not only totally reduce an existing excitation, but, "also carries the condition of the excitable structure to a state farther removed from excitation than is its normal resting one". BALLIF, FULTON and LIDDELL (16, p. 603) come to the same conclusion, when they observe a long suppression of reflex (1—3 sec.) by one single impulse of inhibition, which, according to them, "seems to preclude the possibility that this inhibition is a condition resulting from a WEDENSKY type of interference: *for it continues quite independently of any excitatory process*". SAMOJLOFF (17), too, has similar objections against the first theory, and as we saw, it is the same with the experiences obtained with regard to the Crayfish. In connection, however, with SHERRINGTON's opinion about the peculiar nature of the process of inhibition, he, too, admits the presence of "purily inhibitory" and "purily excitatory" fibres, so that neither this theory may be brought into line with our results.

If we compare the two theories about inhibition, they appear to agree in so far that they have reference to propagated disturbances, which are effected by processes of metabolism in the ganglion-cells and their axons. Whether these disturbances of excitation and inhibition are considered of the same nature and dependent on each other, or a hypothesis is preferred, which considers inhibition and excitation to be independent one by the side of the other, it is evident that no final explanation is arrived at. Moreover, in the observations of decrementless conduction the attention is quite drawn to the disturbance of equilibrium, which is at best variable per axon. By the side of it the "spark" which must bring the "gunpowder"

to explosion, when once the minimum has been reached, is comparatively indifferent. It is, however, not impossible that too much attention paid to the conduction and the neglecting of the question of the basis of the disturbance of equilibrium, may hamper the approximation of the nature of the excitation and inhibition and their relation. It might appear then that not so much the relation between excitation and inhibition is of direct importance, but rather the relation between these two processes and the basis on which both run down. And as soon as we don't only study isolated preparations, but examine the influence on the periphery by a centre, we have already to consider, by the side of the propagated disturbances of equilibrium, the influence on these, by their natural basis situated in the centre. If we stimulate this centre artificially there arises a direct "propagated disturbance", but at the same time we influence that which is the rail for the natural disturbance of equilibrium. Hence the possibility that these two phenomena, which normally are in a fixed relation to each other, cover each other in the final result when there is stimulation. With lower animals, especially with snails, the importance of the distinction mentioned above has distinctly come to light by the investigations of JORDAN. That which must be looked upon as the basis for the "propagated disturbance", is called by JORDAN the „Tätigkeitszustand". That indeed, these two exist by the side of each other, may be proved with the help of the anatomical separation of two ganglien with the snails, viz. the cerebral- and the pedal-ganglion. Whereas stimulations applied to these two ganglien, do not work specifically, but always cause contraction, means, which change the „Tätigkeitszustand" do work specifically, viz. on the cerebral-ganglion they influence the excitability, on the pedal-ganglion the plastic tonus in the muscles.

With the decrementless conduction it may be possible, that the particles, which cause the conduction by metabolism-processes stimulate each other to activity (conduction) without influencing the class of magnitude of the neighbouring particles. KEITH LUCAS compared the decrementless conduction with a match, charged with gunpowder. The particles of gunpowder ignite each other, but the magnitude of metabolism is dependent on the energy, represented by each of the particles of gunpowder, so not on the stimulation. With decrement-conduction it must be different. Here the process of conduction is dependent on the force with which it is caused. Therefore it cannot only depend on the quantity of energy in each reacting particle of the nerve. So each of these particles works in coordination with the preceding particles; besides the processes of activity as such, coordinating factors must be present, by which the reaction of all particles must be made coordinated with each other and dependent on the energy of the stimulation. This coordinating factors might be identical with the „Tätigkeitszustand", which as a basis of the reflexes in central phenomena, does not cause the reflexes themselves, but determines their quantity. According to our opinion inhibition is not founded on "propagated disturbance", but on

a change of the coordinating factor or basis of reaction. Accordingly the influence of the uppercentres does not manifest as a rule itself with *Evertebrata* as a momentary inhibition, but as some state, as we saw.

For the uppercentres with *Vertebrata* such states of activity have long been known. When PAWLOW (19) in connection with quite different things, viz. for the explication of the conditioned reflexes, speaks about "charge" of the centres, and when MAGNUS (20) uses the name "Reflexbereitschaft" for the state in the spinal cord in his classical experiments with the catstail viz. when this contracts in the directions of the bent side, when stimulated, our opinion is with JORDAN, that different names are used here for the same property, viz. that which JORDAN calls in a wider sense "Tätigkeitszustand".

The "strychnine reversal" of the nerves, too, might probably be classed under the same point of view, namely the influencing of the state of activity.

This is not the place to enter further into these things. Though the experiments, which test the value of JORDAN's hypothesis on the crayfish, have not yet been concluded, yet provisional results already point to the importance of this view, also for our group of animals. Moreover there is the insufficiency of the two most important theories of inhibition. If the great difference between the various groups of animals may urge caution, the essential conformity of nature of all central elements makes it extremely probable that also its fundamental expressions agree in the whole animal kingdom.

For the rest the JORDAN-hypothesis opens a new field of research.

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Mathematics. — *On the convergence of continued fractions.* By
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(Communicated at the meeting of September 29, 1928).

1. The elements a_k and b_k of a continued fraction

$$\frac{a_1}{b_1} + \frac{a_2}{b_2} + \frac{a_3}{b_3} + \dots$$

being throughout positive, the discussion of its convergence is at once reduced to an investigation of the character of a determinate series with positive terms. For the convergence of a fraction, all the components of which, with exception of the first, have a negative numerator, such a simple test does not exist¹⁾. In a number of cases the following theorem, founded on the so called extension of a continued fraction, may be applied.

The continued fraction

$$B = \frac{a_1}{b_1} - \frac{a_2}{b_2} - \frac{a_3}{b_3} \dots$$

where a_k and b_k are positive numbers, will converge unconditionally, if it is possible to assign a sequence of positive numbers λ_k , such that not one of the quantities

$$A_1 = b_1 - \lambda_1, \quad A_k = \lambda_{k-1}(b_k - \lambda_k) - a_k \quad (k = 2, 3, 4, \dots)$$

is negative, and that not all of them are equal to zero.

In order to prove this proposition, we have only to transform the convergents. For the first convergent B_1 we may write

$$B_1 = \frac{a_1}{b_1} - \frac{a_1}{A_1} + \frac{\lambda_1}{1}$$

and changing here b_1 into $b_1 - \frac{a_2}{b_2}$, A_1 into $A_1 - \frac{a_2}{b_2}$, the convergent B_1 changes into the second B_2 , hence we have

$$\begin{aligned} B_2 &= \frac{\frac{a_1}{A_1 - \frac{a_2}{b_2}} + \frac{\lambda_1}{1}}{1} = \frac{a_1}{A_1} + \frac{b_2 \lambda_1 - a_2}{b_2} = \frac{a_1}{A_1} + \frac{\lambda_1}{1} + \frac{a_2}{b_2 \lambda_1 - a_2} = \\ &= \frac{a_1}{A_1} + \frac{\lambda_1}{1} + \frac{a_2}{A_2} + \frac{\lambda_1 \lambda_2}{1}. \end{aligned}$$

¹⁾ Encyclopädie der Math. Wissensch., I. 1, p. 130.

Again, replacing b_2 by $b_2 - \frac{a_3}{b_3}$, we get similarly

$$\frac{a_2}{A_2 - \frac{a_3 \lambda_1}{b_3}} + \frac{\lambda_1 \lambda_2}{1} = \frac{a_2}{A_2} + \frac{\lambda_1 (\lambda_2 b_3 - a_3)}{b_3} = \frac{a_2}{A_2} + \frac{\lambda_1 \lambda_2}{1} + \frac{a_3}{\lambda_2 b_3 - a_3} =$$

$$= \frac{a_2}{A_2} + \frac{\lambda_1 \lambda_2}{1} + \frac{a_3}{A_3} + \frac{\lambda_2 \lambda_3}{1}$$

and for the third convergent B_3 we find the expression

$$B_3 = \frac{a_4}{A_1} + \frac{\lambda_1}{1} + \frac{a_2}{A_2} + \frac{\lambda_1 \lambda_2}{1} + \frac{a_3}{A_3} + \frac{\lambda_2 \lambda_3}{1}.$$

In this way we infer that the convergents B_1, B_2, B_3, \dots are identical with the convergents B'_2, B'_4, B'_6, \dots of a new continued fraction

$$B' = \frac{a_1}{A_1} + \frac{\lambda_1}{1} + \frac{a_2}{A_2} + \frac{\lambda_1 \lambda_2}{1} + \dots + \frac{a_m}{A_m} + \frac{\lambda_{m-1} \lambda_m}{1} + \dots$$

According to the properties of the numbers λ_k and A_k the numerator of each of its components is positive and the denominators of the components of odd order are not all of them equal to zero. Therefore, all convergents of B' are positive, and as at least one of the convergents of odd order is a finite quantity, the convergents B'_2, B'_4, B'_6, \dots of even order form an increasing sequence, tending to a finite positive limit. Remembering that the convergent B_n of the original fraction B is equal to the convergent B'_{2n} of the extended fraction B' , the convergence of B is ensured. Necessarily this convergence is unconditional, for after removing an arbitrary number of initial components from the fraction B , the proof of the convergence still holds. The fraction B' may converge or not, if it is convergent, our reasoning shows that in that case $B = B'$.

As an example I select the fraction

$$B = \frac{1^2}{3} - \frac{2^2}{5} + \frac{3^2}{7} - \frac{4^2}{9} + \dots$$

Here we have $a_k = k^2$, $b_k = 2k + 1$ and putting $\lambda_k = k + 1$ we get $A_1 = 1$, $A_k = 0$ and therefore

$$B' = \frac{1}{1} + \frac{2}{1} + \frac{2^2}{0} + \frac{2, 3}{1} + \frac{3^2}{0} + \frac{3, 4}{1} + \dots$$

or

$$B' = \frac{1}{\frac{1}{1}} + \frac{1}{\frac{1}{2}} + \frac{1}{0} + \frac{1}{\frac{1}{3}} + \frac{1}{0} + \frac{1}{\frac{1}{4}} + \dots$$

Now the denominator of the first component of B' is different from zero and the series $\frac{1}{1} + \frac{1}{2} + \frac{1}{3} + \frac{1}{4} + \dots$ diverges, therefore the fraction B' is convergent, and since we have $B'_1 = B'_3 = B'_5 = \dots = 1$, it follows that $B = B' = 1$.

2. Suppose that for a certain set of positive numbers λ_k the quantities A_k satisfy the assigned conditions only, when the index k is large enough.

Then from the fraction B we remove a sufficient number of initial components and extend the fraction

$$C = \frac{a_m}{b_m} - \frac{a_{m+1}}{b_{m+1}} - \frac{a_{m+2}}{b_{m+2}} - \dots$$

Now the extended fraction

$$C' = \frac{a_m}{b_m - \lambda_m} + \frac{\lambda_m}{1} + \frac{a_{m+1}}{A_{m+1}} + \frac{\lambda_m \lambda_{m+1}}{1} + \frac{a_{m+2}}{A_{m+2}} + \dots$$

will no longer contain any negative elements, hence the fraction C is unconditionally convergent, and as we have

$$B = \frac{a_1}{b_1} - \frac{a_2}{b_2} - \dots - \frac{a_{m-1}}{b_{m-1} - C},$$

the behaviour of B will depend upon the value of C and upon the finite set of the numbers a_1, a_2, \dots, a_{m-1} ; b_1, b_2, \dots, b_{m-1} . Take for instance

$$B = \frac{1}{1} - \frac{2}{2} - \frac{3}{3} - \frac{4}{4} - \dots$$

and put $\lambda_k = 2$. As extended fraction we find

$$B' = \frac{1}{-1} + \frac{1}{1} + \frac{2}{-2} + \frac{4}{1} + \frac{3}{-1} + \frac{4}{1} + \frac{4}{0} + \frac{5}{1} + \dots,$$

and we notice three negative elements. Therefore we remove from B the first and the second component and consider the fraction

$$C = \frac{3}{3} - \frac{4}{4} - \frac{5}{5} - \frac{6}{6} - \dots$$

Extending this fraction, always taking $\lambda_k = 2$, we get

$$C' = \frac{3}{1} + \frac{2}{1} + \frac{4}{0} + \frac{4}{1} + \frac{5}{1} + \frac{4}{1} + \frac{6}{2} + \dots$$

All elements of this fraction being positive, the fraction C is unconditional convergent. Replacing the second component of B , we consider the intermediate fraction

$$D = \frac{2}{2} - \frac{3}{3} - \frac{4}{4} - \frac{5}{5} - \dots$$

It is readily seen that this fraction diverges. Indeed, calculating the denominator of the n^{th} convergent in the usual way, we find that it is equal to $n + 1$ and from this result we get for the convergent D_n itself

$$D_n = 1 + 1! + 2! + \dots + (n-1)!.$$

Hence we have $D = \lim_{n \rightarrow \infty} D_n = \infty$, and from

$$D_n = \frac{2}{2 - C_{n-1}}, \quad B_{n+1} = \frac{1}{1 - D_n},$$

it follows that $C=2$ and $B=0$. Thus it is shown that the fraction B converges, but that the convergence is conditional.

3. From what precedes it is seen that as soon as the proposition is applicable, every convergent $B_n = \frac{P_n}{Q_n}$ of the fraction B has a positive denominator Q_n . Conversely, assuming the denominators Q_n of the convergents of a convergent fraction B to be throughout positive, it will be possible to assign a set of positive numbers λ_k , satisfying the required conditions. Indeed, the relation

$$B_{n+1} - B_n = \frac{a_1 a_2 \dots a_{n+1}}{Q_n Q_{n+1}}$$

shows that the convergents B_n form an increasing sequence, hence it follows from a proposition of PRINGSHEIM¹⁾ that the convergence of the fraction B is unconditional, and that therefore the n^{th} remainder

$$r_n = \frac{a_{n+1}}{b_{n+1}} - \frac{a_{n+2}}{b_{n+2}} - \dots$$

is a finite quantity. Writing now

$$B = \frac{(b_n - r_n) P_{n-1} - a_n P_{n-2}}{(b_n - r_n) Q_{n-1} - a_n Q_{n-2}} = \frac{P_n - r_n P_{n-1}}{Q_n - r_n Q_{n-1}},$$

we find

$$r_n = \frac{(B - B_n) Q_n}{(B - B_{n-1}) Q_{n-1}},$$

a result, showing that r_n is positive. If we now take $\lambda_k = r_k$, we find

$$A_1 = b_1 - r_1 = \frac{a_1}{B} > 0, \quad A_k = r_{k-1} (b_k - r_k) - a_k = 0, \quad (k = 2, 3, 4 \dots)$$

and so it is seen that in the case of a convergent fraction B the convergents of which have positive denominators, the remainders r_k may serve as a set of numbers λ_k . By a similar reasoning we can prove for a divergent fraction B , having convergents with a positive denominator Q_n that the fraction

$$\frac{a_2}{b_2} - \frac{a_3}{b_3} - \frac{a_4}{b_4} - \dots,$$

obtained by removing the first component, is unconditional convergent and that it takes the value b_1 .

4. Making about the numbers λ_k various suppositions, we obtain various conditions, each of which is sufficient but not necessary for the unconditional convergence of the continued fraction B .

¹⁾ PERRON. Die Lehre von den Kettenbrüchen, p. 231.

For instance, taking:

1. $\lambda_k = 1$, unconditional converg. is ensured, when: $b_k \geq a_k + 1$.
2. $\lambda_k = a_{k+1}$, " " " " " $b_k \geq a_{k+1} + 1$.
3. $\lambda_k = \frac{1}{2} b_k$, " " " " " $b_k b_{k-1} \geq 4 a_{k-1}$.
4. $\lambda_k = \sqrt{a_{k+1}}$, " " " " " $b_k \geq \sqrt{a_k} + \sqrt{a_{k+1}}$.

As an example I consider the fraction

$$B = \frac{1^{2s}}{1^s + 2^s} - \frac{2^{2s}}{2^s + 3^s} + \frac{3^{2s}}{3^s + 4^s} - \frac{4^{2s}}{4^s + 5^s} + \dots$$

Applying the fourth test, $b_k \geq \sqrt{a_k} + \sqrt{a_{k+1}}$, it is seen that the fraction converges unconditionally. As extended fraction we find

$$B' = \frac{1}{1} + \frac{2^s}{1} + \frac{2^{2s}}{0} + \frac{2^s 3^s}{1} + \frac{3^{2s}}{0} + \frac{3^s 4^s}{1} + \dots$$

or by a slight transformation

$$B' = \frac{1}{\frac{1}{1^s}} + \frac{1}{\frac{1}{2^s}} + \frac{1}{0} + \frac{1}{\frac{1}{3^s}} + \frac{1}{0} + \frac{1}{\frac{1}{4^s}} + \dots$$

Direct calculation of the convergents $B'_n = \frac{P'_n}{Q'_n}$ leads to the results:

$$P'_{2n+1} = Q'_{2n+1} = 1, \quad Q'_{2n} = \sum_1^{n+1} \frac{1}{k^s}, \quad P'_{2n} = Q'_{2n} - 1, \quad B'_{2n} = 1 - \frac{1}{\sum_1^{n+1} \frac{1}{k^s}},$$

Consequently we have $B = \lim_{n \rightarrow \infty} B'_{2n} = 1 - \frac{1}{\zeta(s)}$, in case $s > 1$, and simply $B = 1$, if $s \leq 1$.

5. Lastly, I will apply the extension to the so called regular fraction

$$B = \frac{1}{a_1} - \frac{1}{a_2} + \frac{1}{a_3} - \frac{1}{a_4} + \dots$$

It converges unconditionally, as soon as $a_k \geq 2$, for then the general condition $b_k \geq a_k + 1$ is satisfied. By a suitable choice of the numbers λ_k , however, it can be shown that sometimes convergence is possible even, when $a_k < 2$. In general we have

$$A_k = \lambda_{k-1} (a_k - \lambda_k) - 1$$

and therefore the fraction will converge, if we suppose

$$a_k = \lambda_k + \frac{1}{\lambda_{k-1}}.$$

Now if λ_k slightly exceeds unity and λ_k is less than λ_{k-1} , we may have $\lambda_k + \frac{1}{\lambda_{k-1}} < 2$. So, for instance, we can take $\lambda_k = 1 + \frac{1}{2k+1}$ and this supposition leads to $a_k = 2 - \frac{1}{2k(2k+1)}$. Hence the fraction

$$B = \frac{1}{2 - \frac{1}{2.3}} - \frac{1}{2 - \frac{1}{4.5}} - \frac{1}{2 - \frac{1}{6.7}} - \frac{1}{2 - \frac{1}{8.9}} - \dots$$

is unconditionally convergent. The extended fraction becomes

$$B' = \frac{1}{\frac{1}{2}} + \frac{\frac{4}{3}}{1} + \frac{1}{0} + \frac{\frac{4.6}{3.5}}{1} + \frac{1}{0} + \frac{\frac{6.8}{5.7}}{1} + \dots$$

or

$$B' = \frac{1}{\frac{1}{2}} + \frac{1}{\frac{3}{4}} + \frac{1}{0} + \frac{1}{\left(\frac{3}{4}\right)^2 \frac{5}{6}} + \frac{1}{0} + \frac{1}{\left(\frac{3.5}{4.6}\right)^2 \frac{7}{8}} + \dots$$

and as the divergence of the series

$$\frac{1}{2} + \left(\frac{3}{4}\right) + \left(\frac{3}{4}\right)^2 \frac{5}{6} + \left(\frac{3.5}{4.6}\right)^2 \frac{7}{8} + \left(\frac{3.5.7}{4.6.8}\right)^2 \frac{9}{10} + \dots$$

ensures the convergence of the fraction B' , from the equation $B'_{2n+1} = 2$ we get at once $B = 2$.

6. Sometimes the extension is also serviceable for the investigation of a so called alternate fraction

$$F = \frac{a_1}{b_1} - \frac{a_2}{b_2} + \frac{a_3}{b_3} - \frac{a_4}{b_4} + \frac{a_5}{b_5} - \dots,$$

where the numbers a_k and b_k all are positive. Again, taking a set of positive numbers $\mu_1, \mu_3, \mu_5, \dots$ we transform the convergents as follows. In the first place we have

$$F_1 = \frac{a_1}{b_1} = \frac{a_1}{b_1 - \mu_1} + \frac{\mu_1}{1}$$

and changing b_1 into $b_1 - \frac{a_2}{b_2}$ we get for the second convergent

$$\begin{aligned} F_2 &= \frac{a_1}{b_1 - \mu_1 - \frac{a_2}{b_2}} = \frac{\mu_1}{1} = \frac{a_1}{b_1 - \mu_1} + \frac{\mu_1 b_2 - a_2}{b_2} = \\ &= \frac{a_1}{b_1 - \mu_1} + \frac{\mu_1}{1} + \frac{a_2}{\mu_1 b_2 - a_2}. \end{aligned}$$

Writing $b_2 - \frac{a_3}{b_3}$ in stead of b_2 , the third convergent takes the form

$$F_3 = \frac{a_1}{b_1 - \mu_1} + \frac{\mu_1}{1} + \frac{a_2}{\mu_1 b_2 - a_2} + \frac{\mu_1 a_3}{b_3 - \mu_3} + \frac{\mu_3}{1},$$

and thus we are lead to consider the fraction

$$F' = \frac{a_1}{b_1 - \mu_1} + \frac{\mu_1}{1} + \frac{a_2}{\mu_1 b_2 - a_2} + \frac{\mu_1 a_3}{b_3 - \mu_3} + \frac{\mu_3}{1} + \frac{a_4}{\mu_3 b_4 - a_4} + \\ + \frac{\mu_3 a_5}{b_5 - \mu_5} + \frac{\mu_5}{1} + \frac{a_6}{\mu_5 b_6 - a_6} + \frac{\mu_5 a_7}{b_7 - \mu_7} + \frac{\mu_7}{1} + \dots$$

Evidently every convergent of F is at the same time a convergent of F' and in particular we have the relations

$$F_{2k} = F'_{3k} \quad , \quad F_{2k-1} = F'_{3k-1}.$$

From these equations we conclude that both fractions F and F' will converge or diverge at the same time, and that in the first case we shall have $F = F'$. For in the supposition

$$\lim_{k \rightarrow \infty} F'_{3k} = \lim_{k \rightarrow \infty} F'_{3k-1} = F',$$

we have also

$$\lim_{k \rightarrow \infty} F_{2k} = \lim_{k \rightarrow \infty} F_{2k-1} = F',$$

and when F'_{6k} and F'_{6k+1} do not have the same limit or have no limit at all, the convergents F_{4k} and F_{4k-1} are not approaching the same finite limit and F is a divergent fraction. Now let us suppose that throughout

$$b_{2k+1} - \mu_{2k+1} \geq 0 \quad , \quad \mu_{2k+1} b_{2k+2} - a_{2k+2} \geq 0,$$

a supposition involving the inequality

$$b_{2k+1} b_{2k+2} - a_{2k+2} \geq 0,$$

then the investigation of the alternate fraction F is reduced to that of the fraction F' , all the elements of which are positive. Taking, for instance, the fraction

$$F = \frac{1}{1} - \frac{1}{1} + \frac{1}{2} - \frac{1}{3} + \frac{1}{2} - \frac{1}{5} + \frac{1}{2} - \frac{1}{7} + \dots$$

and putting $\mu_{2k+1} = 1$, we find

$$F' = \frac{1}{0} + \frac{1}{1} + \frac{1}{0} + \frac{1}{1} + \frac{1}{1} + \frac{1}{2} + \frac{1}{1} + \frac{1}{1} + \frac{1}{4} + \frac{1}{1} + \frac{1}{1} + \frac{1}{6} + \dots$$

Now the fraction obtained by removing the three first components,

$$\frac{1}{1} + \frac{1}{1} + \frac{1}{2} + \frac{1}{1} + \frac{1}{1} + \frac{1}{4} + \dots$$

evidently converges and as it is positive, the fraction F and therefore the fraction F' converges also. In order to find the value of F , we remark that the numerator P_{2n+1} and the denominator Q_{2n+1} of the convergents F_{2n+1} of odd order satisfy the equation of finite differences

$$X_n = 2(2n-1)X_{n-1} + X_{n-2},$$

two independent solutions of which can be shown to be

$$H_n = \int_1^\infty e^{-w^2} \frac{N_{2n+1}(w)}{\sqrt{w^2-1}} dw, \quad K_n = \int_0^\infty e^{-w^2} T_{2n+1}(w) dw,$$

where $\frac{T_{2n+1}(w)}{N_{2n+1}(w)}$ is the $(2n+1)$ th convergent of the continued fraction

$$\frac{1}{\sqrt{w^2-1}} = \cfrac{1}{w} - \cfrac{1}{2w} - \cfrac{1}{2w} - \cfrac{1}{2w} - \dots$$

For $n=1$ and $n=2$ we may verify that

$$H_n = \frac{1}{2} e^{-1} \Gamma\left(\frac{1}{2}\right) P_{2n+1}, \quad K_n = \frac{1}{2} \Gamma\left(\frac{1}{2}\right) Q_{2n+1},$$

and therefore these equations hold for all values of n . By now proving

$$\lim_{n \rightarrow \infty} (H_n - K_n) = 0,$$

we get the required result

$$F = \lim_{n \rightarrow \infty} \frac{P_{2n+1}}{Q_{2n+1}} = e \lim_{n \rightarrow \infty} \frac{H_n}{K_n} = e.$$

Mathematics. — *Ein Beitrag zur Theorie der WEYL'schen Übertragung.* By V. HLAVATÝ. (Communicated by Prof. R. WEITZENBÖCK.)

(Communicated at the meeting of September 29, 1928).

§ 1. ¹⁾ Eine WEYL'sche Übertragung W_n kann man bekanntlich als eine affine Übertragung definieren, bei welcher ein Tensor n^{ten} Ranges $g_{\lambda\mu}$ existiert, so dass

$$\nabla_{\mu} g_{\lambda\gamma} = -Q_{\mu} g_{\lambda\gamma} \dots \dots \dots (1)$$

wo Q_{μ} natürlich kein Gradientvektor ist. Nun ist bei der Transformation

$$\bar{g}_{\lambda\mu} = \sigma g_{\lambda\mu} \quad , \quad \sigma = \sigma(x) \dots \dots \dots (2)$$

die Gleichung

$$\nabla_{\mu} \bar{g}_{\lambda\gamma} = -\bar{Q}_{\mu} \bar{g}_{\lambda\gamma} \dots \dots \dots (3)$$

gültig, wo der Vektor \bar{Q}_{μ} durch

$$\bar{Q}_{\mu} = Q_{\mu} - \nabla_{\mu} \log \sigma \dots \dots \dots (4)$$

definiert ist. Der Tensor $g_{\lambda\mu}$ kann also mit einem beliebigen skalaren Faktor multipliziert werden, ohne die durch die Gleichung (1) ausgedrückte Eigenschaft zu verlieren, und unter allen Tensoren, die so entstehen können und die alle einen zugehörigen Vektor Q_{μ} besitzen, ist kein einziger bevorzugt. Eine wirkliche Massgeometrie im RIEMANN'schen Sinne gibt es also in der WEYL'schen Übertragung nicht. Den Vektor Q_{μ} kann man auch folgendermassen schreiben

$$Q_{\mu} = 2/n \left(\Gamma_{\alpha\mu}^{\alpha} - \frac{\partial}{\partial x^{\mu}} \log \sqrt{|g_{\alpha\beta}|} \right) \dots \dots \dots (4a)$$

§ 2. Ganz anders verhält sich die Sache, wenn man die Geometrie längs einer in W_n gegebenen Kurve

$$x^{\nu} = x^{\nu}(t) \quad t_0 < t < t_1 \dots \dots \dots (5)$$

treiben will. Dann kan man folgenden Satz beweisen:

Längs einer in W_n gegebenen Kurve (5) lässt sich immer mittels einer Kwadratur ein Tensor $G_{\lambda\mu}$ $n \cdot n$ Ranges angeben, der der Kurve entlang konstant ist, und bei (2) invariant bleibt:

$$a) \frac{\delta}{\delta t} G_{\lambda\mu} = 0, \quad b) \bar{G}_{\lambda\mu} = G_{\lambda\mu}^2 \dots \dots \dots (6)$$

¹⁾ Zum § 1 vergl.: SCHOUTEN: Der Ricci-Kalkül (Berlin 1924) S. 217.

²⁾ In jeder linearen Übertragung, und also auch in der WEYL'schen, lässt sich ein

Daraus kann sofort gefolgert werden, dass sich längs (5) immer eine Massgeometrie (mit dem Fundamentaltensor $G_{\lambda\mu}$) einführen lässt und letzten Endes, dass man in W_n auch die Frenetschen Formeln *genau* so, wie bei einer RIEMANN'schen Übertragung, angeben kann.

§ 3. Um den oben angegebenen Satz zu beweisen, wollen wir zuerst einen Tensor $q_{\lambda\mu}$ n -ten Ranges aufsuchen, der der Kurve (5) entlang konstant ist und bei (2) sich nur um einen konstanten Faktor abändert. Setzt man

$$q_{\lambda\mu} = g_{\lambda\mu} e^{\int_{t_0}^t Q_{\mu} dx^{\mu}} \dots \dots \dots (7)$$

so ist einerseits

$$\frac{\delta}{\delta t} q_{\lambda\mu} = 0 \dots \dots \dots (8)$$

und andererseits

$$\bar{q}_{\lambda\mu} = \sigma_0 q_{\lambda\mu}, \dots \dots \dots (9)$$

wo σ_0 den Wert der Funktion σ im Punkte $t=t_0$ angibt. Der Tensor $q_{\lambda\mu}$ genügt also wirklich beiden hier aufgestellten Bedingungen. Bezeichnet man mit q die Determinante der Bestimmungszahlen von $q_{\lambda\mu}$ und setzt man $q = \sqrt[n]{\bar{q}}$ so ergibt sich aus (8)

$$\frac{d}{dt} q - \Gamma_{\alpha\mu}^{\alpha} \frac{dx^{\mu}}{dt} q = 0 \dots \dots \dots (10)$$

§ 4. Aus dem Tensor $q_{\lambda\mu}$ können wir eine — längs der Kurve — konstante Tensordichte $q_{\lambda\mu}$ konstruieren, die in Bezug auf (2) invariant ist. Die Funktion q ist eine Dichte vom Gewicht 1 und es gilt für jede Dichte w desselben Gewichtes

$$\frac{\delta}{\delta t} w = \frac{d}{dt} w - \frac{dx^{\mu}}{dt} \Gamma_{\alpha\mu}^{\alpha} w^3) \dots \dots \dots (11)$$

Der Vergleich von (10) und (11) lehrt, dass

$$\frac{\delta}{\delta t} q = 0 \dots \dots \dots (12)$$

und infolgedessen ist laut (8) und (9)

$$q_{\lambda\mu} = q_{\lambda\mu} q^{-\frac{2}{n}} \dots \dots \dots (13)$$

eine Tensordichte, die der oben aufgestellten Bedingungen genügt.

konstantes quadratisches Tensorfeld entlang einer gegebenen Kurve angeben. Dazu ist aber notwendig ein lineares System von $\frac{n(n+1)}{2}$ Differentialgleichungen zu lösen. Hier soll gezeigt werden, dass im Falle der W_n das gesuchte Tensorfeld nur durch eine Kwadratur bestimmbar ist.

³⁾ HLA VATÝ: Théorie des densités dans le déplacement général (Annali di Matematica Serie IV, T. 5, 1927—28, p. 73—83.

§ 5. Aus dieser Tensordichte lässt sich jetzt leicht der Tensor $G_{\lambda\mu}$ gewinnen. Zu diesem Zwecke denken wir uns den kontravarianten n -Vektor aus den (linear unabhängig vorausgesetzten) Vektoren $\frac{\partial x}{\partial t^x} \frac{dx^\nu}{dt}$ ($x=0, \dots, n-1$) längs (5) konstruiert und bezeichnen mit w^{-1} seine einzige von Null verschiedene Bestimmungszahl. Die Funktion w ist eine Dichte vom Gewicht 1 und es gilt also laut (11)

$$\frac{\partial}{\partial t} w = \frac{d}{dt} w - I_{\alpha\mu}^{\alpha} \frac{dx^\mu}{dt} w \quad . \quad . \quad . \quad (11)'$$

Ist φ eine — in Bezug auf (2) — invariante skalare Funktion von t und schreibt man $e = \varphi w$ so ist

$$\frac{\partial}{\partial t} e = \frac{d\varphi}{dt} w + \varphi \frac{\partial w}{\partial t} \quad . \quad . \quad . \quad (14)$$

Ist speziell

$$\varphi = e^{-I} \quad , \quad I = \int_{t_0}^t \frac{dw}{w} = - \int_{t_0}^t I_{\alpha\mu}^{\alpha} \frac{dx^\mu}{dt} dt + [\log w]_{t_0}^t \quad , \quad (15)$$

so ist nach (11)'

$$\frac{\partial}{\partial t} e = 0 \quad . \quad . \quad . \quad (16)$$

Die — in 7) und 15) — angeführten Kwadraturen reduzieren sich dabei, laut (4a), auf eine einzige.

Da $I_{\alpha\mu}^{\alpha}$ und w bei (2) invariant sind, so muss der Tensor

$$G_{\lambda\mu} = q_{\lambda\mu} q^{-\frac{2}{n}} e^n$$

nicht nur der Bedingung (6a), sondern auch der Bedingung (6b) genüge leisten. Um das Feld $G_{\lambda\mu}$ zu bestimmen, hat man wirklich nur eine Kwadratur nötig gehabt. Da $q_{\lambda\mu}$ den Rang n hat so hat $G_{\lambda\mu}$ denselben Rang und der Satz ist also bewiesen.

§ 6. Nimmt man $G_{\lambda\mu}$ als metrischen Tensor längst (5), so besitzt diese Kurve einen ausgezeichneten metrischen, bei (2) invarianten Parameter s ,

$$s = \int_{t_0}^t \left(q_{\lambda\mu} q^{-\frac{2}{n}} e^n \frac{dx^\lambda}{dt} \frac{dx^\mu}{dt} \right)^{1/2} dt \quad . \quad . \quad . \quad (17)$$

den wir als „Bogen“ bezeichnen können. Der Vektor $i_1^\nu = \frac{dx^\nu}{ds}$ ist dann der tangentielle Einheitsvektor (in Bezug auf $G_{\lambda\mu}$) und die Eigenschaft „Einheitsvektor“ zu sein ist gegenüber (2) invariant. Es bestehen dann auch die Frenetschen Formeln⁴⁾

$$\frac{\partial}{\partial s} i_a^\nu = -k_{a-1} i_{a-1}^\nu + k_{a+1} i_{a+1}^\nu \quad (a=1, \dots, n, \quad k_0 = k_n = 0), \quad (18)$$

⁴⁾ STRUIK: Grundzüge der mehrdimensionalen Differentialgeometrie in direkter Darstellung (Berlin 1922), p. 76–78.

Biochemistry. — *The first phases of the chemistry of the dissimilation of the hexoses. (2nd Part).* By A. J. KLUYVER and A. P. STRUYK.

(Communicated at the meeting of October 27, 1928).

§ 1. *Introduction.*

In our first communication under the same title¹⁾ mention was made a.o. of some preliminary experiments which aimed at giving a clearer insight into the nature of the phosphoric esters formed in the so-called "cell-free" fermentation of the hexoses. It appeared from these experiments that the ratio in which hexose-biphosphoric and hexose-monophosphoric esters are present at the end of the phosphorylation period is greatly influenced by the nature of the dried yeast-sample used for the preparation of the maceration juice. The most remarkable result of these experiments was doubtless that in special cases the amount of hexose monophosphoric ester largely exceeded that of hexose biphosphoric ester.

Until we had claimed a hexose monophosphoric ester to be the first reaction product in the dissimilation of hexoses, investigators used to attribute exclusively to the hexose biphosphoric ester an important function in the biochemical degradation of the hexoses²⁾. Thus the schemes representing the chemistry of the dissimilation of the hexoses drafted before 1926 did not include the hexose monophosphoric ester.

It is obvious that the observation mentioned above as to the predominance of the hexose monophosphoric ester under special conditions — observation published at a little earlier date also by NEUBERG and LEIBOWITZ³⁾, who however did not derive important conclusions from it — was quite appropriate to support our theory developed at the end of 1925. But from the very beginning we were quite aware that we might only consider our theory as being confirmed if we should succeed in explaining why under special conditions the hexose monophosphoric ester prevails, whereas under other conditions, as in the majority of the cases examined since HARDEN and YOUNG's classical investigations, the amount of the hexose biphosphoric ester largely exceeds that of the hexose monophosphoric ester. Of course at the same time the question rose in how far our conception of the first phases of the chemistry of the dissimilation of hexoses might offer certain advantages as compared with the other existing theories for the explanation of the signalled diversity in behaviour.

1) These Proceedings 30, 871, (1927).

2) These Proceedings 29, 322, (1926); c.f. too the communication cited above: § 2.

3) C. NEUBERG und J. LEIBOWITZ, Biochem. Z., Bd. 184, 489, (1927).

A short survey will be given of the experiments which show that on the one hand it is possible to control the conditions determining the formation of each of the two esters mentioned and which on the other hand are appropriate to answer in the affirmative the question raised above. For a more detailed description of these experiments we refer to the thesis published in the meantime by one of us (Str.)¹⁾.

§ 2. *Further experiments on the appearance of a hexose monophosphoric ester in "cell-free" fermentation.*

In the course of the experiments of which some examples were already given in our previous paper many observations were made on the ratio of both phosphoric esters present at the end of the phosphorylation period. In doing so we used an improved method of analysis, which was largely due to NEUBERG and LEIBOWITZ (l.c.). As for some modifications introduced by us we refer to the thesis mentioned above.

Table I gives the results of four experiments. In all experiments we used a fermentation mixture composed of 1 part of maceration juice and 1 part of a 5 % solution of Na_2HPO_4 ; the initial concentration of the glucose was always 10 %. In the table V_m indicates the molecular ratio of hexose monophosphoric and hexose biphosphoric ester at the end of the phosphorylation period, viz. at the moment that the rate of fermentation had fallen down to the rate previous to the addition of the phosphate. At this moment the phosphate added appeared to be practically completely esterified. Moreover the maximum rate of production of carbonic acid, in ccm per 5 minutes, observed in the various experiments is included in the table.

TABLE I.

Number of experiment ²⁾	V_m	Maximum rate of production of CO_2 (ccm. per 5 min.)
7	4.6	—
8	3.3	24.9
10A	12.6	14.2
11A	9.8	17.2

These results strike us because in all cases the amount of the hexose monophosphoric ester considerably exceeds that of the hexose biphosphoric ester. Therefore it is necessary to revise our original conception in so far

¹⁾ A. P. STRUYK, *Onderzoekingen over de alcoholische gisting*, Diss., Delft 1928.

²⁾ The numbers correspond to the numbers of the experiments reported in STRUYK's thesis.

that the hexose *monophosphoric* ester of ROBISON may not be considered as the primary product of the phosphorylation of glucose, but has to be taken for a stabilised modification, as has already been earlier suggested by MEYERHOF ¹⁾. For the assumption that ROBISON's *mono*-ester should be the primary reaction product does not go in with the observed downfall of the rate of development of carbonic acid at the end of the phosphorylation period in those cases in which nearly all the phosphate may be recovered as *mono*-ester.

The attention is drawn to the fact, already underlined in our previous communication, that the maximum rate of production of carbonic acid is higher in as much as the ratio of the two phosphoric esters changes in favour of the *biphosphoric* ester. However even in experiment 8, the curve of which shows a pronounced top, the amount of the *biphosphoric* ester is still far less than that of the *monophosphoric* ester.

Nevertheless in trying to reproduce similar experiments under exactly the same conditions as chosen by ROBISON we came across various cases in which the hexose *biphosphoric* ester predominated and in which the amount of the *monophosphoric* ester corresponded with the amount estimated by ROBISON at about 15 % of the total phosphate esterified.

In examining the differences in the conditions underlying these various experiments we were struck first of all by the fact that, although in both cases the initial concentration of the phosphate was the same, ROBISON used the maceration juice in higher concentration than we did in our experiments. Thus the concentration of the catalytic principles in the experiments of ROBISON was higher.

Therefore we came to suppose that the same maceration juice would convert the inorganic phosphate added more or less in one of the two phosphoric esters depending on the concentration in which the juice was applied. A higher concentration of "active zymase" would increase the yield of *biphosphoric* ester.

The experiments gave a complete confirmation of this view.

A maceration juice which applied at an earlier date in a concentration of

TABLE II.

Number of experiment	Concentration of the maceration juice	V_m	Indication of the corresponding curves
14	0.67	2.4	C
13	0.56	8.4	B
12	0.50	16.4	A

¹⁾ O. MEYERHOF, Die Naturwissenschaften, **14**, 1179, (1926); c.f. too: O. MEYERHOF und K. LOHMANN, Biochem. Z. **185**, 113, (1927).

0.81 led to a value for $V_m = 0.34$ gave the results reproduced in Table II when applied in lower concentrations.

The attention may be drawn to the fact — as appears from Fig. 1 — that the observed change in the ratio of both phosphoric esters is accompanied by a pronounced change in the nature of the curves which represent the rate of development of the carbonic acid during the phosphorylation period.

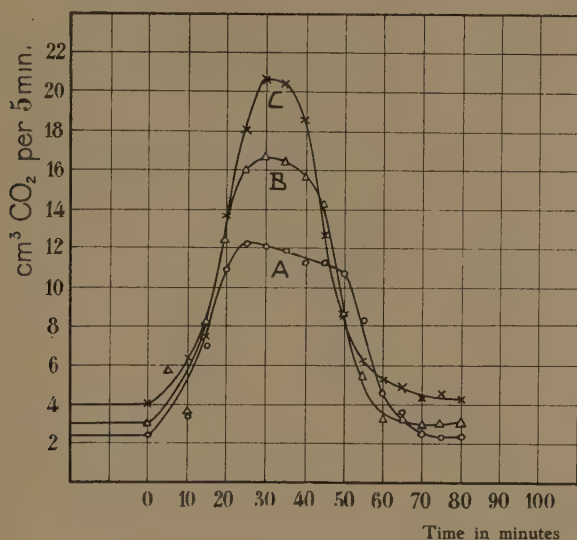


Fig. 1.

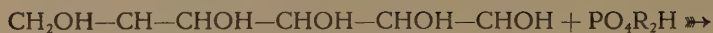
Apparently there is a close connection between the two phenomena mentioned in so far as the type with the pronounced top changes into the "flat type" when the *monophosphoric* ester predominates.

§ 3. *Explanation of the observed phenomena on the basis of the scheme adopted for the chemistry of alcoholic fermentation.*

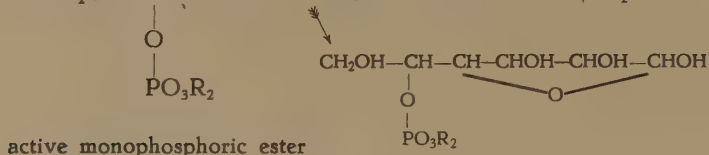
It was already pointed out in our previous communication that the scheme for the chemistry of alcoholic fermentation adopted by us seemed quite appropriate to explain the changes in ratio of both phosphoric esters during "cell-free" fermentation. Further down this matter will be subject to a closer consideration.

First of all the scheme developed in our earlier papers will be reproduced here once more as a whole. As for the position to be given to ROBISON's hexose *monophosphoric* ester the remarks made in § 2 will be taken into account.

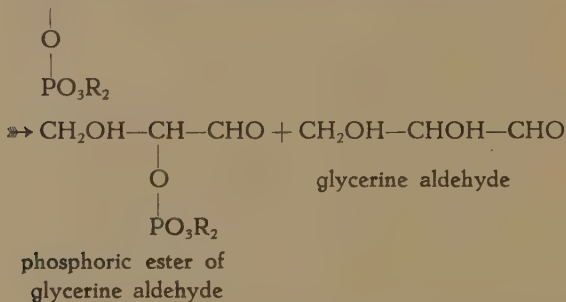
I. Initiating phosphorylation.



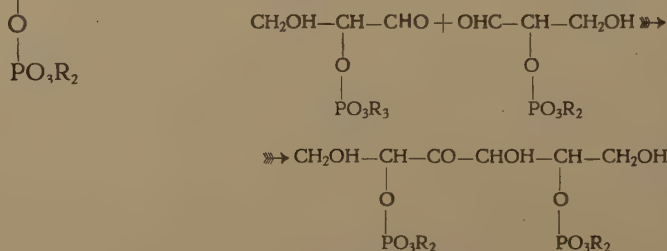

 d-glucose



II. Oxidoreduction of the hexosephosphoric ester.



III. Hydrolysis of the triosephosphoric ester.



The first case of transference of an intermediate product from one agent to the other is met with when the primary product of phosphorylation formed under the influence of the phosphatase (reaction I) must be split under normal conditions by the oxidoreducase according to reaction II. Any falling back of the reducase in this direction will result in an accumulation of the primary product of reaction. This will then be stabilised as ROBISON's hexose *monophosphoric ester*. Thus a part of the phosphate will be withdrawn from the normal cycle of fermentation.

The second case of transference of an intermediate product from one agent to the other is offered when the triosephosphoric ester formed under the influence of the oxidoreducase will have to be split into triose and phosphoric acid by the phosphatase according to reaction III. Any shortcoming of the latter agent will primarily lead to an accumulation of the triosephosphoric ester. On the basis of the arguments given in our previous communication a continued contact of this ester with the oxidoreducase will result in a condensation of the ester to hexose *biphosphoric ester*. This too means a deviation of a part of the phosphate from the normal cycle.

However another part of the phosphate will continue its normal course in "cell-free" fermentation as well and start a new cycle. Thus during the phosphorylation period the fermentation will proceed with increased rate as long as the total quantity of added phosphate has not yet arrived at the side-ways mentioned ¹⁾.

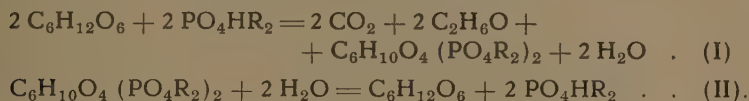
It needs no further explanation that the results obtained with the maceration juices of different origin are in excellent agreement with the above considerations. If in the process of isolation of the catalytic agents from the cells one of the agents has been more damaged than the other, one may expect that in some instances one stabilised product will prevail, in other instances the other. Furthermore it may logically be derived from the following that a decrease of the concentration of "active zymase" in a fermentation medium will give a higher yield of ROBISON's *mono ester*. A more pronounced disturbance of the co-operation of both agents will cause in first instance slower transference of the intermediate products. This implies for the primary product of hexose dissimilation an increased chance for stabilisation in the form of ROBISON's *mono-ester*. As the intermediately formed triose phosphoric ester has no chance of stabilising as such, this ester will as yet — may be retarded — remain subject to the action of the phosphatase. This process will even be favoured, in comparison with what occurs in media with more concentrated zymase, because the greater dilution will promote the escape of the triose phosphoric ester from the sphere of action of the oxidoreducase which tends to bring about a condensation of this ester to hexose *biphosphoric ester*.

¹⁾ The rate of fermentation at the end of the phosphorylation period will thus be conditioned by the rate at which phosphate is split off from the stabilised esters present.

§ 4. *Quantitative examination of the scheme adopted and of other theories concerning the chemistry of the dissimilation of the hexoses.*

It seemed desirable to look out for a quantitative experimental test of the scheme adopted and of the other existing theories concerning the chemistry of the dissimilation of hexoses. This being possible may be derived from the following very condensed survey of the views of other investigators.

10. *The classical theory of HARDEN and YOUNG.* As has been observed more than once in our previous communications this theory can be summarized by the following equations :



Although it is difficult to grant any reality in chemical direction to these symbols, it must be acknowledged that the requirements in quantitative respect, drawn up by the authors some 20 years ago for the course of "cell-free" fermentation, are duly laid down in these equations. At the one hand it is expressed clearly that at the end of the phosphorylation period the whole of the inorganic phosphate may be recovered as hexose biphosphoric ester, at the other hand the production of one molecule of alcohol and of one molecule of carbonic acid is inevitably bound up with the conversion of one molecule of inorganic phosphate into the biphosphoric ester.

It is obvious that the simple fact of the appearance of a hexose *mono*-phosphoric acid demonstrates the inadequacy of the formulation mentioned above. As long as the amount of this ester is small in comparison with that of the *biphosphoric* ester it is easy to understand that there will be a tendency to ascribe the formation of the *monophosphoric* ester to secondary factors.

20. *The modified view of HARDEN and HENLEY*¹⁾. In a recent publication these authors have tried to reconcile the new points of view with the classical theory. In the first place they are inclined to ascribe the appearance of the hexose *monophosphoric* ester partly to a direct esterification of the hexose, a process occurring independently from the main process. In the second place the authors are willing to accept the possibility that part of the *monophosphoric* ester will be NEUBERG's ester and thus will originate from a hydrolysis of the *biphosphoric* ester.

As for the first point it must be observed that then in the cases studied by us, in which the value for *V_m* was generally very high (till 16), the by-process has grown into the main process. Anyhow it will be clear, that

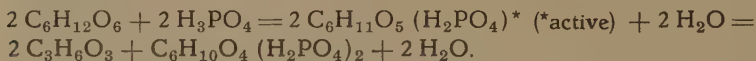
¹⁾ A. HARDEN and F. R. HENLEY, *Biochem. J.* **21**, 1216, (1927).

in the supposition made the requirement $\text{CO}_2/\text{esterified P} = 1$ is no longer in need of fulfilment, but that the requirement $\text{CO}_2/\text{biphosph. ester} = 2$ still must be maintained.

As for the second point experiments have shown conclusively that the hydrolysis of the *biphosphoric* ester during the phosphorylation period is so small that only small deviations of the ratio $\text{CO}_2/\text{biphosphoric ester}$ can be accounted for in this way. Moreover NEUBERG and LEIBOWITZ (l.c.) succeeded in identifying a *monophosphoric* ester produced under similar conditions for no less than 90 % as ROBISON's ester.

Thus even in accepting the view of HARDEN and HENLEY the requirement may be maintained that the ratio $\text{CO}_2/\text{biphosphoric ester}$ will be equal to, or only slightly larger than, 2.

30. *The theory of MEYERHOF.* It was already observed in our previous paper that medio 1926 the above author drew up a new representation of the chemistry of the first phases of the dissimilation of the hexoses. Soon after this MEYERHOF¹⁾ gave the following formulation of his views :



At this occasion MEYERHOF expressed the opinion — which was taken over in our scheme — that ROBISON's *monophosphoric* ester was a stabilised form of the primary reaction product of glucose.

It is obvious that this mode of view in comparison with that of HARDEN and YOUNG has the advantage that arbitrary quantities of *monophosphoric* ester can be formed along with the *biphosphoric* ester. Thus there is no necessity for a fixed proportion $\text{CO}_2/\text{esterified P}$. In contrary to this it must be observed that according to MEYERHOF's scheme too in alcoholic fermentation — where the $\text{C}_3\text{H}_6\text{O}_3$ of the equation will be split quantitatively into CO_2 and $\text{C}_2\text{H}_6\text{O}$ — the proportion $\text{CO}_2/\text{biphosphoric ester}$ must be equal to 2.

40. *The theory of VON EULER and MYRBÄCK*²⁾. In recent time the latter authors have advanced a new view concerning the first phases of the process under consideration. The most essential part of their theory is doubtless that the primary reaction of hexose dissimilation "eine Reaktion darstellt die von derselben Natur ist wie die Aldehyddismutation"³⁾.

The principal argument raised by the Swedish investigators is to be found in their observations that firstly the co-enzyme of alcoholic fermentation acts in a phase preceding that of the phosphorylation and that secondly this very principle is identical with the "co-mutase", a principle indispensable in the mutation of aldehydes by dried yeast preparations.

¹⁾ O. MEYERHOF, Die Naturwissenschaften, **14**, 1175, (1926).

²⁾ C.f. the summary of H. VON EULER, K. MYRBÄCK und R. NILSSON, Ergebnisse der Physiologie, **26**, 531, (1928).

³⁾ H. VON EULER und K. MYRBÄCK, Zeitschr. f. physiol. Chemie, **165**, 38, (1927).

It will suffice to refer to our communication on the heterogeneous nature of the principles indicated by various investigators as "co-enzyme" ¹⁾ for explaining why we cannot accept this argumentation as fully convincing. However a closer analysis of the considerations of VON EULER and MYRBÄCK can be regarded as premature, since the recent investigation of NEUBERG and SIMON ²⁾ has made the identity of "co-enzyme" and "co-mutase" very doubtful. Moreover NEUBERG and SIMON rightly criticize the equalization of a process as the dismutation of aldehydes and of the introductory phase of hexose dissimilation in the scheme of VON EULER and collaborators, since in the last process no oxidoreduction occurs.

For these various reasons a further discussion of the views of VON EULER and MYRBÄCK may be omitted here.

From the preceding survey it results that the three former theories all require the occurrence of a definite ratio between the carbonic acid produced in surplus during the phosphorylation period and either the amount of phosphate esterified or the amount of biphosphoric ester formed.

In contrary to this a reference to § 3 will suffice to show that our mode of view does not bring with it any requirements regarding the ratio of carbonic acid and total phosphate esterified. As for the ratio of carbonic acid and biphosphoric ester formed the only requirement is a minimum value of 2, but much higher values may be reasonably expected.

In Table III a summary is given of the results of a series of experiments

TABLE III.

	Ratio $\frac{\text{monophosph. ester}}{\text{biphosph. ester}}$	Ratio $\frac{\text{carbonic acid}}{\text{esterified P.}}$	Ratio $\frac{\text{carb. acid}}{\text{biphosph. ester}}$
HARDEN and YOUNG	0	1	2
HARDEN and HENLEY	indefinite	< 1	2
MEYERHOF	indefinite	≤ 1	2
KLUYVER and STRUYK	indefinite	≥ 1	≥ 2
Experiment 12	16.4	0.60	11.4
" 13	8.4	0.71	7.5
" 14	2.4	0.72	3.2
" 16	0.34	0.89	2.2
" 17	3.6	0.67	4.0
" 18	2.1	0.71	2.9
" 19	0.93	0.82	2.4

¹⁾ These Proceedings 30, 569, (1927); Biochem. Z. 201, 212, (1928).

²⁾ C. NEUBERG und E. SIMON, Biochem. Z. 199, 232, (1928).

which aimed at testing whether the requirements derived from the different theories did hold good. To render the results more easily accessible the meant requirements are put at the head of the table.

For the details of the method of determination of the figures given in Table III we refer to the thesis of STRUYK. It must be kept in mind however that the figures of the carbonic acid produced in the phosphorylation period have been subject to a post-experimental correction as the changes of the concentration of hydrogen ions during the process had been neglected.

Even when taking into account the small inaccuracy of the results owing to this circumstance, there can be no doubt that in many cases the ratio between carbonic acid produced in surplus and the biphosphoric ester formed is considerably larger than 2. In addition attention may be drawn to the fact that also in the paper of HARDEN and HENLEY instances may be found where this ratio exceeds 2. In one case even a value as high as 3.45 was found, a result which HARDEN and HENLEY themselves characterize as inexplicable ¹⁾.

These results are quite incompatible with the different theories advanced by the various investigators. Now we are quite aware that the foregoing does not yield a direct proof for the correctness of our scheme, but we want to emphasize here that our mode of view is up till now the only one which is in perfect agreement with all observations made on the chemistry of "cell-free" fermentation.

Moreover it may be observed that our theory is the only one which brings a logical nexus between "cell-free" fermentation and the fermentation caused by living yeast cells. For in the latter case the ratio of carbonic acid produced and the amount of phosphate esterified — which equals zero — is infinite large, a possibility anticipated in our scheme and in the requirements derived from it.

§ 5. *Final remarks.*

Although the preceding paragraphs only deal with observations on the chemistry of alcoholic fermentation of the hexoses there can be no doubt — taking into consideration the experiences of EMBDEN and MEYERHOF — that the considerations given regarding the first phases of this process apply as well to the first phases of the dissimilation of hexoses by the muscular tissue of animals. The same opinion is expressed in many of the papers of VON EULER. Moreover it seems highly probable that the same holds good for the dissimilation of hexoses by sugar fermenting bacteria of various groups.

The fact that in all these processes the conversion of intermediately

¹⁾ C.f. l.c. p. 1222. The fact, that HARDEN and HENLEY did not get the high values obtained by us, finds its cause in the circumstance that these authors applied higher concentrations of active zymase (zymin-preparations).

formed triose takes different courses does not alter at all the point of view given.

For these reasons we felt justified to give this publication — as well as the preceding one — the general title chosen.

Finally it may be emphasized that this paper only brings a preliminary rounding off of the views given in the two preceding communications in which many arguments may be found which could not be repeated here. A more ample discussion of all problems concerned is given in the thesis of STRUYK.

*From the Laboratory for Microbiology of the
Technical University.*

Delft, October 1928.

Physiology. — *Investigation on the function of the heart of Maja verrucosa.* By S. DE BOER. (Communicated by Prof. B. BROUWER).

(Communicated at the meeting of October 27, 1928).

The results of this investigation are shortly as follows:

1. A great many investigators (WEBER, BRANDT, ECKHARD, DOGIEL, PLATEAU) had settled, that the refractory stage is wanting during the systole. CARLSON only found a decrease of the irritability, but very strong stimuli also caused summation in the beginning of the systole.

Because the existence or non-existence of a refractory stage has a fundamental significance for the function of the heart I first investigated this point. I carried out this investigation by means of suspension curves. In this case we register the mechanograms only of a part of the heart. Therefore I placed the electrodes, by which induction-shocks were sent in to the heart as near as possible to the point of the heart, which was connected to the lever. Only in this way — and former investigators did not take that into account at all — are accurate results to be obtained.

Contrary to the earlier investigators I found that the heart of *Maja verrucosa* is refractory in the beginning of the systole, even if two accumulators (each of 2 Volts) were present in the primary circuit and the secondary bobbin was quite pushed in.

2. When I caused an extrasystole in a regularly pulsating heart, the rhythm was not disturbed: the following systole started at the same time, in which it would have appeared, had I not caused an extrasystole. The result was the same, when I applied very strong stimuli or when I caused 3 or 4 extrasystoles between two normal systoles. I mean that this result may be better understood, if we accept the neurogenic theory in the heart of *Maja verrucosa*.

3. Hearttetanus arises after faradic stimulation as former investigators also found. In my experiments the tetanus was as high as the normal systoles in other cases high.

4. Very often I found alternation of the heart, which probably was caused by the non-contraction of a part of the heartmuscle.

5. Fractionated systoles also appeared during the alternation. These fractionated systoles arose, when after the small alternationsystole the excitation-wave was propagated through that part of the heartmuscle, which did not contract during the small systoles. I also found these fractionated systoles when an inductionshock was applied to the heart, directly after the refractory stage.

6. When contractility had decreased, it could again increase after moistening with seawater, the osmotic pressure of which is about the

same as that of the blood of *Maja*. This increase of contractility means an improvement of the metabolic condition of the heart-muscle. I made use of this result for my second investigation, which I performed in the heart of *Maja*.

7. I demonstrated in 1915, that alternation of the ventricle arises after warming of the sinus venosus of the frog's heart. Alternation of the ventricle immediately appeared after moistening the sinus venosus by means of warmed solution of RINGER. The alternation was caused by an acceleration of the excitationwaves after the warming. But in this heart we do not know anything about the point, where the excitationwaves arise (pacemaker). Therefore I moistened the whole heart with seawater (30° C.). Here the effect was quite different. In stead of an acceleration of the heart-beat and an alternation, here the heart temporarily stopped beating. Then the contractions started again at a slower rate, whereas contractility had decreased. This initial result of the sudden warming greatly resembles a Vagus-effect. Afterwards acceleration of the systoles arose, which is directly caused by the warming of the heart-muscle or probably it is an accelerans-effect. Indeed BOTTAZZI found in *Maja* inhibiting as well as accelerating nerves.

This communication has been published more extensively in *Zeitschr. für vergleichende Physiologie*, 1928. Vol. 7, p. 445.

Investigation on recurring systoles and fibrillation in Maja.

After having first investigated the normal function of the heart of *Maja verrucosa*, I started this second investigation. I performed this investigation with this animal just because the A-V-connecting systems are here absent, therefore the specific tissue is wanting, in which according to HERING, HABERLANDT (and recently ROTBERGER as well) fibrillation and also recurring systoles should arise under the influence of very frequent excitations. Moreover *Maja* seemed to me so suitable for this purpose, because the heart shows a fairly regular pentagonal form, and the duration of the refractory stage is so short. Here the circumstances are therefore as favourable as possible for the circulating contractionwaves to arise and to continue. The experimental arrangement was the same as in the first investigation. The results are shortly as follows:

1. Recurring systoles as well as fibrillation arise very easily in this heart. Sometimes it is already present directly after the suspension, in other cases it arises at a later moment. If we moisten the heart at regular intervals with seawater, it may arise after many hours, if we do not moisten it anymore, it often arises after some time. The metabolic condition must be bad in the dehaemetised heart before recurring systoles or fibrillation appear. Recurring systoles and fibrillation may also stop spontaneously, the last contraction is then often enlarged and forms a refractory dam (obstacle) at which the circulating wave stops.

2. I was able to cause fibrillation or recurring systoles in the deheame-tised heart of the frog, by means of an inductionshock immediately after the refractory stage. The experiment succeeds quite well also in the heart of *Maja*, but here the stimulus may also be applied at a somewhat later moment.

If however we apply the stimulus at a much later moment, the experiment does not succeed here either, but a normal extrasystole arises. That the experiment succeeds here within much wider limits after the refractory phase, must be ascribed to the fact, that the refractory phase of the normal systole has such a short duration here.

3. Fibrillation and recurring systoles have ordinarily a much longer duration in *Maja* than in the frog's heart. This longer duration is caused by the short refractory phase und by the peculiar form. Chiefly owing to the very short duration of the refractory phase, the circulating contraction wave has less chance of stopping at its own refractory phase.

4. The frequency of the oscillations may change very much during recurring systoles. (from 50 to 120). These differences will be explained in a more extensive communication. Fibrillation, recurring systoles and the normal rhythm may also change every moment.

5. Recurring systoles may also here be stopped by an induction shock. In this way a second contractionwave is set up in a direction opposite to that of the circulating contractionwave. Both are extinguished because the duration of each of the two contractionwaves is shorter than the duration of the refractory phase of the other.

6. I demonstrated in an earlier investigation that quinine makes the metabolic condition of the heart muscle bad. I ascribed the stopping of fibrillation by means of quinine to a deterioration of the metabolic condition.

I predicted that fibrillation (or recurring systoles) might also be stopped by an amelioriation of the metabolic condition because it had become evident from my investigations that fibrillation does not start before the heartmuscle has deterioriated to a certain extent.

This experiment succeeded perfectly with *Maja*. We know from my first investigation with *Maja*, that the metabolic condition of the heart of *Maja* may be amelioriated when we moisten it with seawater. Well then fibrillation or recurring systoles may be stopped when we moisten the heart of *Maja* with seawater. The normal rhythm appears after this.

7. Fibrillation of the hearts of vertebrates may be caused by faradic stimulation. These relations are quite the reverse in the case of *Maja*. If we apply here faradic stimulation tetanus arises and not fibrillation. If however we apply faradic stimulation during fibrillation of this heart, tetanus arises and afterwards the normal rhythm sets in again. We must ascribe this to the short duration of the refractory phase. In this way summation to tetanus may occur. If now such a tetanus is caused during fibrillation, the whole heart becomes refractory and at this refractory phase the circulating contraction wave stops.

This communication has been published more extensively in German in *Archivio di Scienze Biologiche*, Vol. XII, 1928, p. 510.

Investigation on the heartrhythm of Scyllium canicula.

I investigated the deviations of the normal heartrhythm of sharks (*Scyllium canicula*) because these deviations are not often studied in hearts of fishes. The results are the following:

1. The first and most evident difference with the frog's heart and also with the hearts of other vertebrates is this that the heart of *Scyllium* so easily shows dissociation between the activity of the ventricle and that of the auricle.

2. A complete compensatory pause arises after an artificial extrasystole of the ventricle. That was a known fact.

3. ENGELMANN found a complete compensatory pause after an artificial extrasystole of the auricles of the frog's heart. Because the compensatory pause is often abbreviated after extrasystoles of the auricles of mammals, WENCKEBACH's explanation of ENGELMANN's discovery is that in the frog's heart a sinus venosus exists as a separate heartsection and that in the heart of mammals the excitation waves arise in the right auricle. But I certainly found in the frog's heart an abbreviated compensatory pause after premature artificial extrasystoles of the auricles and a more pronounced abbreviation when the stimulus was applied at an earlier period. It was important to try this experiment here too because in the heart of *Scyllium* the sinus venosus exists as a separate heartsection. The result was that the compensatory pause after an artificial extrasystole of the auricles is usually abbreviated and the more so the earlier the stimulus was applied.

The explanation is the same as in the case of the frog's heart.

4. Causing an extrasystole of the auricles at every heart cycle at an anticipated (premature) moment of the period of the auricle, we were able to sustain artificially the halved rhythm of the ventricle.

5. We are able to cause fibrillation or recurring systoles of the ventricle by an inductionshock immediately after the refractory stage. Fibrillation or recurring systoles of the ventricle may also be caused indirectly viz. after a premature extrasystole of the auricle. The excitationwave (contractionwave) which travels along the A-V connecting systems and enters into the ventricular muscle immediately after the refractory phase, causes fibrillation or recurring systoles of the ventricle. If then the excitation-wave enters into the ventricular muscle at a later period, a premature systole of the ventricle is caused.

6. Fibrillation of the auricle in which the rhythm of the sinus venosus is also disturbed may arise after a premature stimulus applied to the auricle.

7. If heartblock (dissociation between auricle and ventricle) exists,

fibrillation of the ventricle may easily be caused, because the sinus excitations do not then disturb it.

8. Alternation of the ventricle may arise after warming the sinus venosus and afterwards it may pass to the halved rhythm of the ventricle.

The normal rhythm returns again after cooling the sinus venosus. After warming the sinus venosus bigeminy of the ventricle may also arise, because disturbances of conduction in the *A-V*-connecting systems arise here much easier. This bigeminy of the ventricle is caused by the fact that every third systole of the ventricle does not appear.

9. STRAUB found that the auricle and the ventricle usually pass to the halved rhythm at the same time after poisoning by antiarin; only in some cases he could show with any certainty that a systole of the ventricle did not arise after a systole of the auricle. He concludes from this that the toxicity of the auricle and the ventricle for antiarin in the hearts of *Selachii* is the same.

The heart of *Scyllium canicula* after dehaemetising does not behave so. Then I found as a rule the halved rhythm of the ventricle at the same time when the rhythm of the auricle remained the same as before. This happened spontaneously as well as after warming the sinus venosus. As a matter of fact I cannot agree with the conclusion of STRAUB at all. When the auricle and the ventricle pass to the halved rhythm at the same time one must not conclude from this fact that toxicity of the ventricle and auricle for antiarin is the same. The result observed by STRAUB means that the auricle passes to the halved rhythm by antiarin: the halved rhythm of the ventricle is then inevitable, because from this moment only half of the impulses travel along the *A-V*-connecting systems from the auricle to the ventricle. Therefore in the experiments of STRAUB the halved rhythm of the ventricle is not caused by antiarin poisoning of the ventricular muscle.

It is therefore impossible after this investigation to compare the toxicity of the ventricular muscle for antiarin with that of the auricle as STRAUB does. In my opinion the halving of the rhythm of the auricle in the experiments of STRAUB is not caused by the toxicity of the auricular muscle for antiarin either. I mean to say that in STRAUB's experiments antiarin acts on the connective systems between sinus and auricle. Indeed STRAUB performed most of his experiments with exstirpated hearts and the sinus venosus with the surrounding tissue suffers very much from the excision. If we leave the heart *in situ*, the conditions for the function of the sinus venosus and the connective systems between sinus and auricle are much more favourable.

This communication has been published more extensively in German in *Publicazioni della Stazione Zoologica di Napoli*, Vol. IX, p. 43, 1928.

Mathematics. — *Eine Verallgemeinerung des Alexanderschen Dualitätssatzes.* By E. R. VAN KAMPEN. (Communicated by Prof. W. VAN DER WOUDE).

(Communicated at the meeting of October 27, 1928).

Der Alexandersche Dualitätssatz ¹⁾ besagt: Ist ein Komplex C eingebettet im n -dimensionalen euklidischen Raum R^n (ergänzt durch einen Punkt), so ist

$$\begin{aligned} P_0(C) - 1 &= P_{n-1}(R^n - C) \\ P_i(C) &= P_{n-i-1}(R^n - C) \quad (i = 1, \dots, n-2) \\ P_{n-1}(C) &= P_0(C) - 1 \quad 2) \quad 3) \end{aligned}$$

L. PONTRJAGIN ⁴⁾ hat diesen Satz folgendermassen verschärft und verallgemeinert:

Eine Basis für die i -Zyklen in C (bezw. für $i=0$ für die i -Zyklen die aus einer geraden Anzahl von Punkten bestehen) und eine ebensolche Basis für die $n-i-1$ -Zyklen in $R^n - C$ können so gefunden werden dass jeder Zykel der ersten Basis mit genau einem Zykel der zweiten Basis verschlungen ⁵⁾ ist.

Betrachtet man für alle Dimensionen nur die Zyklen in C bzw. in $H - C$, die $\neq 0$ in H sind, so gilt derselbe Satz nicht nur für R^n , sondern auch für beliebige unberandete Mannigfaltigkeiten.

Zweck dieser Note ist, anzugeben, wie man diesen Satz verallgemeinern kann auf Komplexe C die in einer beliebigen Mannigfaltigkeit H mit oder ohne Rand R eingebettet sind. "Eingebettet" heisst hier, dass man ein topologisches Abbild von C auf einer Teilmenge von H betrachtet, aber so, dass diese Teilmenge den Rand R von H nicht trifft.

Die Verallgemeinerung lautet:

¹⁾ J. W. ALEXANDER, A proof and extension of the JORDAN-BROUWER separation theorem. (Tr. Am. Math. Soc. 23 (1922) S. 333).

²⁾ $P_i(L)$ heisst: die i -dimensionale Zusammenhangszahl von L ; diese Zusammenhangszahlen, Berandungsrelationen, u.s.w. sind alle modulo 2 zu nehmen. Für: " L^i ist Rand von L^{i+1} " wird geschrieben: $L^{i+1} \rightarrow L^i$. Für alle diese Begriffe siehe: O. VEBLEN, Analysis Situs, The Cambr. Colloquium, Cambridge (Mass.) 1922.

³⁾ Bei ALEXANDER treten die Glieder -1 bei den P_0 nicht auf, da er eine andere Definition der nullten Zusammenhangszahl als die gewöhnliche zugrunde legt. Er betrachtet als geschlossene nulldimensionale Komplexe nur gerade Anzahlen von Punkten.

⁴⁾ L. PONTRJAGIN. Zum Alexanderschen Dualitätssatz, erste und zweite Mitteilung (Gött. Nachr. 1927, S. 315 und S. 446).

⁵⁾ Für die Bedeutung der Verschlingungszahlen und Kroneckerindices siehe § 1 dieser Arbeit.

SATZ V.⁶⁾ Eine Basis für die i -Zyklen in C kann man folgendermaßen aufstellen:

1⁰. Eine Basis für die i -Zyklen in C , die $\neq 0$ sind in H . Dazu gibt es ein ebenfalls vollständiges System von gleichvielen $n-i-1$ -Zyklen in $H-C$, die $\neq 0$ in H sind, von denen aber keine Linearkombination in $H-C$ homolog einem Zykel des Randes von H ist, so dass die Matrix der Verschlingungszahlen der i -Zyklen mit den $n-i-1$ -Zyklen eine Einheitsmatrix ist.

2⁰. Ein System von i -Zyklen in C , von denen keine Linearkombination $\neq 0$ ist in H , die aber alle homolog Randzyklen von H sind. Zu ihnen gibt es ein ebenfalls vollständiges System von gleich vielen $n-i-1$ -Randzyklen von H , $\neq 0$ in H , nicht $\neq 0$ in $H-C$. Die Kroneckerindizes des i -Systems mit dem in H von den $n-i-1$ -Zyklen berandeten $n-i$ -System bilden eine Einheitsmatrix.

3⁰. Ein System von i -Zyklen in H , von denen keine Linearkombination homolog einem Randzykel von H ist. Zu diesen gibt es ein ebenfalls vollständiges System von gleichvielen $n-i$ -Zyklen in H , von denen keine Linearkombination homolog einem $n-i$ -Zykel von $H-C$ ist, so dass die Matrix der Kroneckerindizes eine Einheitsmatrix ist. (Diese Basiselemente von H haben keine Repräsentanten in $H-C$: sie werden von C "zerschnitten").

Für unberandete Mannigfaltigkeiten (wo das Teilsystem 2⁰ fortfällt) besagt dieser Satz etwas mehr als die Pontrjaginsche Sätze, die ausser dem oben zitierten zweiten Satz nur noch eine Zahlenrelation aussagen.

Hieraus kann man leicht Anzahlrelationen ableiten. Wir nennen die Anzahlen der Basiselementen unter 1⁰, 2⁰. und 3⁰: α_i , β_i und γ_i und l_i die Anzahl der i -Zyklen von R die in H unabhängig sind.

Ein vollständiges System von Basiselementen für die i -Zyklen von $H-C$ entsteht, wenn man diejenigen nimmt, die $\neq 0$ sind in H und dazu diejenigen von H , die nicht von C "zerschnitten" werden; man bekommt also:

$$P_i(H-C) = P_i(H) - \gamma_{n-i} + \alpha_{n-i-1} + \beta_{n-i-1}.$$

Weiter hat man natürlich:

$$P_i(C) = \alpha_i + \beta_i + \gamma_i$$

$$P_i(H) - l_i \equiv \gamma_{n-i}$$

$$P_i(R) - l_i \equiv \beta_{n-i-1}.$$

Ein interessantes Nebenresultat der Untersuchung ist die folgende Verallgemeinerung des Poincaréschen Reziprozitätsgesetzes und des bekannten daran anschliessenden Satzes von VEBLEN⁷⁾:

⁶⁾ Satz V enthält auch einen von H. KNESER aufgestellten "topologischen Zerlegungssatz". (Proc. Kon. Ak. Amsterdam 27 S. 601). Die von KNESER daraus hergeleitete Folgerung, dass eine dreidimensionale Mannigfaltigkeit, deren erste Zusammenhangszahl gleich Null ist, nur sphärische Randflächen haben kann (Gött. Nachr. 1925, S. 128) ist auch sofort aus Satz U abzulesen.

⁷⁾ O. VEBLEN, Trans. Am. Math. Soc. 25 (1923), S. 540.

SATZ U. Eine Basis der i -Zyklen in einer berandeten Mannigfaltigkeit H mit Rand R kann folgendermassen gefunden werden:

1⁰. Ein System von i -Zyklen L_i , von denen jeder homolog einem Randzykel ist. Dazu gibt es ein ebenfalls vollständiges System von gleichvielen Randzyklen $L_j^{n-i-1} \neq 0$ in H , etwa $L_j^{n-i} \rightarrow L_j^{n-i-1}$, derart dass $\chi(L_j^{n-i}, L_k) = \delta_{jk}$.

2⁰. Ein System von i -Zyklen, von denen keine Linearkombination homolog einem Randzykel ist. Dazu gibt es ein ebenfalls vollständiges System von gleichvielen $n-i$ -Zyklen mit derselben Eigenschaft, so dass die Matrix der Kroneckerindices eine Einheitsmatrix ist. Hieraus kann man die folgenden Anzahlrelationen ableiten:

$$\begin{aligned} p_i(H) - l_i &= p_{n-i}(H) - l_{n-i}; \\ p_i(R) &= l_i + l_{n-i-1} = p_{n-i-1}(R). \end{aligned}$$

Die Anordnung der Paragraphen ist wie folgt: §§ 1, 2 enthalten ohne Beweis einige im Prinzip bekannte Angaben über Kroneckerindices und über den Einfluss der Einbettung einer Zelle auf den Zusammenhangszahlen einer Mannigfaltigkeit. § 3 enthält einen Hilfssatz, der implizite schon bei ALEXANDER benutzt wird. § 4 bringt eine Teilaussage von V , mit deren Hilfe in § 5 Satz U und in § 6 Satz V bewiesen werden.

Die Beweise sind hier nur angedeutet. Eine genaue Ausführung wird an anderer Stelle erscheinen.

Meinen wärmsten Dank möchte ich Herrn B. L. v. D. WAERDEN aussprechen für seine Hilfe bei der richtigen Formulierung vieler Sätze und Ueberlegungen und für die Angabe einiger Vereinfachungen im Beweisgang.

§ 1. Der Kroneckerindex zweier Komplexe L^k und L^{n-k} (d. h. stetiger Bilder von Komplexen) wird folgendermassen definiert: Man setze voraus dass die Abstände L^k -Rand von L^{n-k} , L^{n-k} -Rand von L^k und Durchschnitt $L^k \cdot L^{n-k} \cdot R$ alle grösser als eine Zahl d sind. Man approximiere die beiden Komplexe derart, dass der Abstand eines Punktes zum approximierenden Punkte immer kleiner ist als $\frac{1}{2}d$, und dass die L^k approximierenden Zellen auf einer Unterteilung von H liegen und die L^{n-k} approximierenden auf der (überall ausser am Rande existierenden) dualen dazu. Dann haben je zwei Zellen von L^k und L^{n-k} entweder einen inneren Punkt oder nichts gemein. Die modulo zwei reduzierte Anzahl dieser Schnittpunkte ist dann der Kroneckerindex⁸⁾. Er ist unabhängig von der gewählten Approximation und hat folgende Eigenschaften:

- I. $\chi(L^k, L^{n-k}) = \chi(L^{n-k}, L^k)$;
- II. $\chi(L^k, L_1^{n-k} + L_2^{n-k}) = \chi(L^k, L_1^{n-k}) + \chi(L^k, L_2^{n-k})$;
- III. Treffen L^k und L^{n-k} sich nicht, so ist $\chi(L^k, L^{n-k}) = 0$;
- IV. Ist $L^{k+1} \rightarrow L^k$ und $L^{n-k} \rightarrow L^{n-k-1}$, so ist $\chi(L^k, L^{n-k}) = \chi(L^{k+1}, L^{n-k-1})$.

⁸⁾ Für eine ausführliche Darstellung im allgemeinen Fall (d. h. nicht modulo 2 und ohne Beschränkung auf zwei Dimensionen deren Summe genau n ist) siehe S. LEFSCHETZ, Trans. Am. Math. Soc. 28 (1926), S. 1, Part. I.

Daraus folgt für $L^{n-k-1} = 0$:

V. Ist $L^k \neq 0$ und $L^{n-k} \rightarrow 0$, so ist $\chi(L^k, L^{n-k}) = 0$.

Diese Sätze ermöglichen die Definition der Verschlingungszahl $v(L^k, L^{n-k-1})$, wenn L^k und L^{n-k-1} zueinander fremd und beide $\neq 0$ sind. Sei nämlich $K^{k+1} \rightarrow L^k$; dann setzen wir

$$v(L^k, L^{n-k-1}) = \chi(K^{k+1}, L^{n-k-1}).$$

Nach V ist diese Definition unabhängig von der speziellen Wahl von K^{k+1} ; aus IV folgt weiter

$$v(L^k, L^{n-k-1}) = v(L^{n-k-1}, L^k).$$

§ 2. Der Einfluss einer eingebetteten Zelle auf den Zusammenhangszahlen einer Mannigfaltigkeit H mit Rand R wird bestimmt durch folgenden

SATZ O⁹⁾: Bettet man in H eine 'Zelle C^i ein und ist L^{k-1} fremd zu C^i und Rand von L^k in H , so ist (ausgenommen wenn $k=n$) L^{k-1} auch $\neq 0$, etwa Rand von K^k in $H-C^i$, so dass $K^k \neq L^k$ in H . Im Ausnahmefall ist entweder L^{k-1} auch Rand von L^k in $H-C^i$ oder $L+R$ Rand von $H-L^k$ in $H-C^i$.

Da dieser Satz gültig bleibt für $L^{k-1} = 0$, so enthält er die Tatsache, dass es zu jedem $L^k \rightarrow 0$ ein zu C^i fremdes K^k L^k gibt, ausgenommen wenn $R = 0$ und $L^k = H$ ist.

§ 3. HILFSSATZ T_i . Es seien gegeben eine Zelle $C^i \rightarrow S^{i-1}$ und ein Komplex $L^k \rightarrow L^{k-1}$, der erste ohne, der zweite evtl. auch mit Singularitäten eingebettet in H , derart dass L^k zu S^{i-1} und L^{k-1} zu C^i fremd ist. Dann ist entweder $k=n-i$, $\chi(C^i, L^k) = 1$ oder es gibt ein zu C^i fremdes ' L^k ', derart dass $L^{k-1} + L^k$ unberandet und Rand von L^{k+1} ist, wobei noch L^{k+1} in einer willkürlichen ε -Umgebung von C^i gewählt werden kann, dabei aber immer eine von ε unabhängige Mindestentfernung d von S^{i-1} behält.

SATZ P_i : S^i sei eine 'Sphäre $\neq 0$ in H . Dann gibt es einen Zykel $L^{n-i-1} \neq 0$ in H , verschlungen mit S^i . Dieses L^{n-i-1} bildet, zusammen mit dem Rand R von H , falls H berandet ist, eine Basis für die Zyklen aller Dimensionen in $H-C$, die $\neq 0$ in H sind.

Satz und Hilfssatz werden durch gleichzeitige vollständige Induktion bewiesen auf Grund der folgenden zwei Ueberlegungen:

a. Aus P_{i-1} folgt T_i (T_0 ist klar). Nach O existiert (ausgenommen für $k=n$) der dort definierte K^k mit der Eigenschaft $L^k + K^k \neq 0$ in H . Nach P_{i-1} ist (bis auf den Sonderfall in Hilfssatz T_i) nun auch $L^k + K^k$ (oder für $k=n-1$ evtl. $L^k + K^k + R$) $\neq 0$ in $H-S^{i-1}$, etwa Rand von ' L^{k+1} '.

Die Zellen einer ε -Unterteilung von ' L^{k+1} ', die C^i treffen, bilden einen Komplex $L^{k+1} \rightarrow L^k$. Sei ' $L^k = L^k + {}''L^k$ '. Dann ist ${}''L^k = L^k + {}'L^k \pmod{2}$

⁹⁾ Für Beweise siehe: J. W. ALEXANDER, a. a. o.¹⁾ S. 340.

nach Konstruktion $\neq 0$, und auch die Entfernungsbedingungen sind erfüllt, etwa mit d = Entfernung von S^{i-1} zu L^{k+1} . Bleibt noch zu zeigen, dass $'L^k$ die Zelle C^i nicht trifft. Setzt man $'L^{k+1} = L^{k+1} + ''L^{k+1}$, so ist $''L^{k+1}$ ein Komplex, der C^i nicht trifft, und dessen Rand genau $'L^k + K^k$ (oder $'L^k + K^k + R$) ist. Addiert man zu diesem Rand mod 2 den Komplex $K^k (+R)$, der ebenfalls C^i nicht trifft, so erhält man $'L^k$.

b. Aus T_i folgt P_i . Wir zerlegen S^i in zwei Zellen A, B , die sich längs S^{i-1} treffen. Im Fall $i \neq 0$ sei L^{n-i} der mit S^{i-1} verschlungene Komplex; im Fall $i = 0$ sei $L^{n-i} = H$. In beiden Fällen ist $\chi(L^{n-i} A) = 1$. L^{n-i} trifft A und B in fremden abgeschlossenen Mengen, die eine Entfernung $d > 0$ besitzen. Von einer $d/2$ -Unterteilung von L^{n-i} nehmen wir die Zellen, die A treffen; sie bilden einen Komplex $L_A^{n-i} \rightarrow L^{n-i-1}$. Nach 1, I, II, III gilt:

$$\begin{aligned} 1 &= \chi(L^{n-i}, A) = \chi(L_A^{n-i}, A), \\ &= \chi(L_A^{n-i}, A + B) = \chi(L_A^{n-i}, S^i) = \nu(L^{n-i-1}, S^i). \end{aligned}$$

Also ist L^{n-i-1} mit S^i verschlungen. Ist ein $L^k \neq 0$ in H , etwa Rand von L^{k+1} , und fremd zu S^i , so kann man nach O voraussetzen, dass L^{k+1} zu B fremd ist. (Eventuell nach Ersetzung von L^k durch $L^k + R$ und von L^{k+1} durch $L^{k+1} + H$). Aus T folgt nun unmittelbar dass L^k bzw. $L^k + R$ in $H - C \neq 0$ oder $\neq L^{n-i-1}$ ist.

§ 4. SATZ Q. Der Komplex C sei in H eingebettet.

Eine Basis der i Zyklen von C kann man folgendermassen aufstellen:

1°. Eine Basis für die i Zyklen in C , die $\neq 0$ sind in H . Dazu gibt es eine Basis von gleichvielen $n-i-1$ Zyklen in $H - C$, $\neq 0$ in H , sodass die Matrix der Verschlingungszahlen eine Einheitsmatrix ist.

2°. Ein System von i Zyklen, von denen keine Linearkombination $\neq 0$ ist in H und wozu es ein (zusammen mit dem System unter 1°. vollständiges) System von $n-i-1$ Zyklen in $H - C$, $\neq 0$ in H , gibt, sodass die Matrix der Kroneckerindices des i Systems mit einem willkürlichen von den $n-i-1$ Zyklen berandeten $n-i$ System eine Einheitsmatrix ist.

3°. Ein (zusammen mit dem System unter 2°. vollständiges) System von i Zyklen, von denen keine Linearkombination $\neq 0$ ist in H . Dazu gibt es in H ein System von gleichvielen $n-i$ Zyklen, sodass die Matrix der Kroneckerindices eine Einheitsmatrix ist. Jeder Zykel in H ausser diesen hat einen homologen in $H - C$.

BEWEIS. Wir nehmen an, der Satz sei bewiesen für denjenigen Komplex B , der aus C durch Weglassung des Innern einer Zelle A von der höchsten in C vorkommenden Dimension i entsteht. Der Rand von A (also der gemeinsame Teil von A und B) sei S^{i-1} . Genau wie beim Beweis von "Aus T_i folgt P_i " konstruieren wir $L_A^{n-i} \rightarrow L^{n-i-1}$ so, dass L_A^{n-i} zu B fremd und $\chi(L_A^{n-i}, A) = 1$ ist. Drei Fälle:

a. Sei S^{i-1} nicht $\neq 0$ in B . Bei der Konstruktion von L^{n-i-1} gehe man aus von dem nach Induktionsannahme (1°) existierenden Zykel L^{n-i} in $H - B$,

der $\neq 0$ in H und mit S^{i-1} verschlungen ist. Dann ist offenbar $L^{n-i-1} \neq 0$ in $H - C$, während es in $H - C$ kein $'L^{n-i} \neq L^{n-i}$ (die Homologie ist in $H - B$ zu verstehen) gibt. Es ist also ein mit S^{i-1} verschlungener $^{n-i}$ Zykel, der in $H - B$ vorhanden war, verloren gegangen in $H - C$, während man sich mit Hilfe von T überzeugt, dass sich sonst in den Zusammenhangszahlen und Verschlingungsrelationen nichts geändert hat.

b. Ist S^{i-1} Rand von L^i in B , sodass $L^i + A \neq 0$ in H , so ist L^{n-i-1} mit $L^i + A$ verschlungen. Jeder $^{n-i}$ Zykel in $H - B$ musz dann nach § 1, V mit A den Kroneckerindex 0 haben, ist also nach T zu ersetzen durch einen in $H - B$ homologen, der C^i nicht schneidet. Mit T überzeugt man sich weiter, dass ausser dem neu hinzugekommenen L^{n-i-1} sich nichts in $H - C$ gegenüber $H - B$ geändert hat.

c. Sei S^{i-1} Rand von L^i in B , aber es sei unmöglich, L^i so zu wählen, dass $L^i + A \neq 0$ in H . Dann ist entweder:

c_1 : $L^{n-i-1} \neq 0$ in $H - C$, etwa Rand von $'L^{n-i}$. Dann hat $'L^{n-i} + L_A^{n-i}$ den Kroneckerindex 1 mit A , also auch mit $A + L^i$. Man überzeugt sich weiter wie vorhin, dass dieses $'L^{n-i} + L_A^{n-i}$ das einzige Basiselement von $H - B$ ist, das bei Übergang zu $H - C$ verloren geht.

c_2 : L^{n-i-1} nicht $\neq 0$ in $H - C$. Man hat $(L^i + A, L_A^{n-i}) = 1$. Es soll bewiesen werden, dass man ein $'L^i$ finden kann, so dass $(L^i + A, 'L^{n-i}) = 0$ für jedes $'L^{n-i} \rightarrow L^{n-i-1}$. $'L^{n-i}$ entsteht aus L_A^{n-i} durch Addition eines $^{n-i}$ Zykels. Man soll also $'L^i$ in $B \rightarrow S^{i-1}$ so wählen dass $\chi('L^i + A, L^{n-i}) = 0$ für jeden $^{n-i}$ Zykel L^{n-i} , wobei man natürlich L^{n-i} jederzeit durch eine homologe ersetzen darf. Trifft $L^{n-i} B$ nicht dann ist entweder $\chi(L^i + A, L^{n-i}) = 1$ oder $= 0$. Wendet man aber im ersten Fall T an auf $L^{n-i} + L_A^{n-i}$, dann folgt gegen Voraussetzung $L^{n-i-1} \neq 0$ in $H - C$. Im zweiten Fall ist es schon in Ordnung. Man kann sich also weiter beschränken auf die unter 3⁰ in Satz Q genannten $^{n-i}$ Zyklen. Ist q ihre Anzahl und gibt es mindestens einen für den $\chi(L^i + A, L^{n-i}) = 1$ ist, dann kann man ihre Basis $L_1^{n-i}, \dots, L_q^{n-i}$ so annehmen, dass $\chi(L_a^{n-i}, L^i + A) = 0$, wenn $a = 1, \dots, q - 1$ und $= 1$, wenn $a = q$. Es gibt dann aber einen $'L^i$ Zykel $'L^i$, so dass $(L_a^{n-i}, 'L^i) = 0$ für $a = 1, \dots, q - 1$ und $= 1$ für $a = q$. Es ist klar dass man $'L^i = L^i + ''L^i$ nehmen kann. Wie vorhin beweist man leicht die weiteren Aussagen von Q für C .

Baut man nun C , von einer endlichen Anzahl von Punkten ausgehend, allmählich auf unter Hinzufügung von Zellen immer höherer Dimension, deren Rand jeweils schon vorhanden ist, so folgen alle Behauptungen von Satz Q.

§ 5. Wir wenden Q an auf dasjenige Gebilde K , welches man bekommt, wenn man an H längs R das STEINITZsche Product von R mit einer Strecke anheftet, während wir als eingebetteten Komplex das ursprüngliche H nehmen. Fall 1⁰ von Q kommt nun offenbar nicht in Betracht; Fall 3⁰ liefert: Ein $'L$ Zykel von H , der mit jedem $^{n-i}$ Zykel von H den Kroneckerindex 0 hat, ist homolog einem Randzykel, oder: zu jeden $'L$ Zykel in H nicht homolog einem Randzykel gibt es einen $^{n-i}$ Zykel, so dass

sie zusammen den Kroneckerindex 1 haben. Das ergibt, wenn man es für die Basis ausspricht, die zweite Hälfte von Satz *U*. Für das in Satz *Q* unter 2^0 genannte System bleibt nur übrig das System der Randzyklen von H , nicht ~ 0 in H . Mit ihm ist in $K - H$ verknüpft ein System, homolog dem System der Randzyklen von H , ~ 0 in H . Das ergibt die erste Hälfte von Satz *U*.¹⁰⁾

§ 6. Vergleichen wir Satz *Q* mit Satz *U* so folgt:

a. Das i System von Q , 3^0 . ist ein Teil des Systems *U*, 2^0 .

b. Das i System von Q , 2^0 . ist homolog einem Randsystem von H , da ja sonst nach *U* die Eigenschaft der dort genannten Matrix, eine Einheitsmatrix zu sein, durch Addition eines bestimmt gewählten $n-i$ Zyklus zerstört werden könnte.

c. Nunmehr folgt auch, dass man das $n-i-1$ System von Q , 2^0 . durch ein Randsystem ersetzen darf da es noch Satz *U* ein Randsystem gibt dass allen betreffenden Bedingungen genügt.

Damit ist aber der ganze Satz *V* bewiesen.

¹⁰⁾ Der Gedanke dieses Beweises verdanke ich Herrn B. L. VAN DER WAERDEN.

Physics. — *Adsorption of iodine on calciumfluoride.* By J. H. DE BOER.
(Communicated by Prof. G. HOLST.)

(Communicated at the meeting of February 25, 1928.)

In case of a heteropolar crystal-lattice one has to expect that the ions at the surface of a crystal exert an electrical field still outside the crystal. This field is at distances comparable with the dimensions of the ions, so strong that dipoles are attracted noticeably. Neutral atoms or molecules, not in possession of a dipolmoment, will be polarised by this field, as a consequence of which also these atoms or molecules are attracted perceptibly. In the following it will be shown that in fact thin layers of salt are able to bind neutral atoms, to the effect that *adsorption* of these atoms on the layer of salt takes place.

This phenomenon also plays an important part in different industrial applications.

Indeed, in the manufacturing of electrical lamps the blackening of the wall of the bulb by evaporated tungsten in vacuum lamps is usually counteracted for instance by introducing some salt or other into the bulb ¹⁾). Sometimes a chemical reaction is used, e.g. in case of K_3TiCl_6 . This substance is able to split off chlorine, by which the tungsten, precipitated as a consequence of evaporation of the filament, is bound. In other cases, however, the salt exerts only a physical action, as has been shown by L. HAMBURGER, G. HOLST, D. LELY and E. OOSTERHUIS ²⁾). This is especially so in case of various heteropolar inorganic salts, which crystallise in coordination-lattices. Examples of such salts are (L. HAMBURGER and others, loc. cit.) $NaCl$ and CaF_2 . Originally these salts are brought on the filaments and after that evaporated to the wall of the bulb. So, for example, on glowing the filaments at about $2000^\circ C$. in vacuum, CaF_2 evaporates and is deposited on the wall of the bulb in the form of a thin, invisible layer of salt with a very large surface.

On closer investigation of the causes of this physical action, the question arose: of what order of magnitude is the electrical field which is brought about by the ions at the surface of such a thin layer of salt. We intended to find out whether a neutral atom, which is present above such a layer at a distance, comparable with the dimensions of the atoms, can be polarised by this field to a marked degree.

Before entering into the experiments, carried out in order to answer the

¹⁾ See for example: G. HOLST, *Elektrische Lichtbronnen* V. U. B. 1920.

²⁾ *Proc. Roy. Acad. Amsterdam* 21, 1078 (1919).

above-mentioned question, we shall try first of all to show by calculation that the forces, exerted by the ions at the surface of the salt, are indeed strong enough to cause such an effect.

On account of the fact that parallel to the cube-face of CaF_2 alternating layers of calcium- and fluorine-ions are present, one could expect that the surface of CaF_2 was built up out of either only positive, or only negative ions. The outermost ions, however, are drawn to the inside by the layers of ions lying under them, while, on the other hand, they themselves draw these layers a little into their own direction. Therefore, for the sake of simplicity, we shall in the following suppose that the surface of CaF_2 is built up out of both positive and negative ions, which ions form the twodimensional lattice represented in fig. 1; in this figure the larger circles represent the calcium-ions, the smaller ones the fluorine-ions.

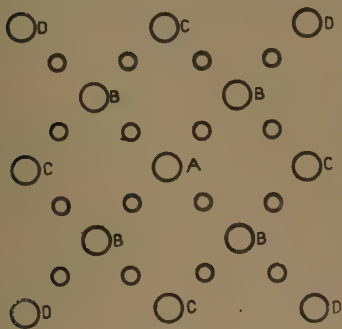


Fig. 1.

Let us suppose that a polarisable atom is present above the calcium-ion A, at a distance $a \times r$; r is the distance of a calcium-ion from the nearest fluorine-ion. In this polarisable atom a dipole will be generated, as is indicated in fig. 2. The generated dipole, the moment of which is P , will



Fig. 2.

be attracted by the ion A. As a consequence of this process, an amount of energy, equal to

$$\frac{2ep}{a^2 r^2},$$

is gained. The dipole is also attracted by an ion B (fig. 2); there are four of them (fig. 1). The energy gained per ion, is:

$$\begin{aligned} & \frac{2ep}{(PB)^2} \cos BPA = \\ & = \frac{2ep}{r^2} \cdot \frac{a}{(a^2 + 2r^2)^{3/2}} \end{aligned}$$

Taking into account all the calcium-ions, the energy becomes:

$$\varphi_1 = \frac{2aep}{r^2} \sum \{a^2 + (2n)^2 + (2m)^2\}^{-3/2} = S_1 \frac{ep}{r^2},$$

In this formula, n and m represent arbitrary integral numbers, both positive and negative, including zero. The fluorine-ions act in the opposite direction; for their action a similar sum can be written down. Thus the total energy of the dipole is obtained as the difference of two series of terms; this difference converges rather rapidly.

In figure 3 the numbers $S = S_1 - S_2$ (S is the factor by which $\frac{ep}{r^2}$ must be multiplied in order to obtain the total energy) are given as a function of the distance, between the polarisable atom and the layer of ions¹).

As can be seen in the figure, this sum S diminishes rapidly with increasing distance the atom.

Apart from this energy of attraction between the generated dipole and the field of the ions, we have to consider the energy, necessary for the generation of the dipole. This energy amounts to

$$\frac{p^2}{2a},$$

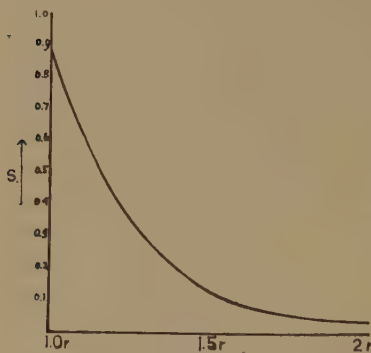


Fig. 3.

where a represents the polarisability of the atom. The total amount of energy (gained energy will be counted as negative) becomes therefore :

$$\eta = -S \frac{ep}{r^2} + \frac{p^2}{2a} \quad ^2)$$

A condition for the equilibrium, is :

$$\frac{\partial \eta}{\partial p} = 0$$

therefore :

$$p = a \frac{Se}{r^2}$$

by which the expression for the energy changes to :

$$\eta = -S^2 \cdot \frac{e^2 a}{2 \cdot r^4}.$$

With iodine as the polarisable atom, and CaF_2 as the salt (compare the experiments, discussed below), we can determine the order of magnitude

¹) We intend to recur to this calculation, and also to the following considerations and calculations, more in detail elsewhere.

²) We do not take into consideration BORN's repulsion forces.

of q . For the polarisability of the iodine-atom we assume the value to be $5 \cdot 10^{-24}$ 1); the distance r is in this case $1.93 \cdot 10^{-8}$ cm. According to V. M. GOLDSCHMIDT 2) the radius of the calcium-ion is equal to $1.06 \cdot 10^{-8}$ cm, and that of the iodine-atom $1.35 \cdot 10^{-8}$ cm. It follows from these figures that the distance from Ca^{++} to I equal to $1.25 r$. As fig. 3 shows, in this case $S = 0.36$. Thus for the energy with which an iodine-atom is attracted, we obtain the value:

$$\varphi = -(0.36)^2 \cdot \frac{(4.77)^2 \times 5}{2 \times (1.93)^4} \cdot 10^{-12} \text{ erg.}$$

Per grammatom this becomes 7600 cal., a rather large energy. The dipole-moment, which, according to this view, would be generated in the iodine, amounts to

$$p = 2.3 \cdot 10^{-18} \text{ e.s.e.,}$$

that is of the same order of magnitude as the dipole-moment of water 3).

Thus, if vapour of iodine (or other gases or vapours which are polarisable) are present above a surface of such a salt, atoms (or molecules) of iodine will be bound at the surface; this means, vapour of iodine will be *adsorbed* to the thin layer of salt 4).

The formation of a mono-molecular adsorbed layer can thus be explained with the add of the foregoing considerations. The question arises now whether only one layer can be bound by adsorption. Another iodine-atom, on the top of the first one, is not subjected to any noticeable attraction from the underlying field of the ions, on account of its large distance. This is clear from figure 3. The dipole of the first iodine-atom however, will generate a dipole also in this second iodine-atom, and this latter dipole in its turn will act upon the first one. Thereupon a third, a fourth, and so on, iodine-atom can be bound as a consequence of polarisation. The adsorption of more than one layer thickness will thus be represented by fig. 4 or fig. 5, which figures do not need a further explanation.

On account of the fact that both the iodine-atoms in the first layer and the atoms in the next layers exert influence on the binding of the first layer, the energy deduced higher-up is too large. If, in fig. 4, we take into

1) The polarisability of the gaseous, non-deformed iodine-ion is equal to $7.5 \cdot 10^{-24}$; see K. FAJANS and G. JOOS, Zts. f. Physik **23**, 1 (1924).

2) V. M. GOLDSCHMIDT, Ber. d. d. chem. Ges. **60**, 1263 (1927).

3) The dipole-moment of water is equal to about $2 \cdot 10^{-18}$ e. s. u.

4) In the meantime also O. BLÜH and N. STARK, Zts. f. Phys. **43**, 575 (1927) and also E. HÜCKEL, Adsorption und Kapillar-Kondensation, Leipzig, Ak. Verlagsges. 1928, have given similar explanations for the forces, which play a part in the adsorption. The first-mentioned authors arrive at the same conclusion as we do, viz. that the adsorption needs not to be limited to a mono-atomic layer. We have waited to publish our point of view till the experiments gave a sufficient confirmation.

account only the atoms of the first layer, then the energy per grammatom is already less, because all the dipoles of the first layer repel each other thus we obtain an energy of 3450 cal. per grammatom. In case we include in the reckoning also the reaction of the following layers on the first one.



Fig. 4.



Fig. 5.

we obtain something like 3750 cal. These calculations ought to be considered as approximations, giving only an idea of the order of magnitude, because, for example, we do not know what is the distance of the first layer of iodine-atoms to the second layer.

In the case of fig. 4 as well as in that of fig. 5, it can be calculated that the magnitude of the dipole in successive layers diminishes regularly, according to the following formula ¹⁾:

$$p_n = K^{n-1} \cdot p_1$$

if p_n represents the dipole of an atom in the n^{th} layer, p_1 that of an atom in the first layer; K is a constant, which depends on the distance of the iodine-atoms, their polarisability and contains constants of summation.

The energy of binding between successive layers also diminishes regularly:

$$\varphi_n = (K^2)^{n-1} \varphi_1.$$

In such an adsorbed system the energy of the attractions and repulsions between the dipoles will increase the heat of evaporation; in fact, the n^{th} layer, which is in equilibrium with the vapour above the adsorbed system, is bound by an energy, equal to:

$$\varphi_{\text{evap.}} + \varphi_n.$$

With regard to this layer, the relation must hold:

$$\ln \pi = \frac{-(\varphi_{\text{evap.}} + \varphi_n)}{RT} + B$$

if π represents the pressure of the iodine-vapour in equilibrium with the adsorbed system. In case π approaches the pressure of saturation π_0 at the temperature under consideration, n will increase; if $\pi = \pi_0$, n will

¹⁾ The following calculations will be published elsewhere more in detail, in collaboration with Dr. C. ZWIKKER.

become infinite. In this case φ_n is equal to zero, so that the ordinary equation for the vapour-pressure :

$$\ln \pi_0 = -\frac{\varphi_{\text{evap.}}}{RT} + B$$

will hold. If the two equations are subtracted from each other, we obtain :

$$\ln \frac{\pi}{\pi_0} = -\frac{\varphi_n}{RT}.$$

Substitution of the expression for φ_n gives :

$$\ln \frac{\pi}{\pi_0} = -\frac{(K^2)^{n-1} \varphi_1}{RT} = C \cdot K_1^{n-1}$$

In this equation C and K_1 are two constants, if the temperature of the adsorbed system remains constant. Thus this equation represents an *adsorption-isotherm* for the adsorption in a layer of more than one molecule thickness.

We are going to describe now some experiments, which are in accordance

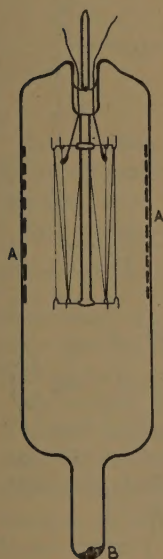


Fig. 6.

with the above-given considerations. In the apparatus, represented in fig. 6, calciumfluoride is present on the wall of the glassbulb opposite to the filament. This CaF_2 has been obtained by evaporation from the filament. There is solid iodine at B . We choose iodine, in the first place because it can easily be obtained in state of vapour, and further because it would be easily polarisable (higher-up we assumed for the polarisability the value 5.10^{-24}). Besides it is coloured, and it can be determined quantitatively without difficulty. If now the iodine at B is cooled by means of liquid air, there is practically no vapour of iodine in the apparatus and no perceptible adsorption (the layer of calciumfluoride is invisible). If then the temperature at B is raised to for example 0° , the pressure of the vapour of iodine corresponds to that of 0° , that is 0.027 mm. As a consequence of this iodine is deposited at A and there it appears as a brown, transparent layer. Keeping A at room-temperature and raising the temperature of B will make grow the layer thicker, until, if B too is brought to room-temperature, distillation of iodine takes place (this process is influenced

by small fluctuations in the temperature). In this case small *crystals* of iodine are formed on the wall of the glass-bulb, also on spots where there is no calciumfluoride.

Thus we can regulate the pressure of the vapour of iodine π by keeping

B at different temperatures. If now the quantity of iodine on the CaF_2 is determined analytically, we are able to study the relation between this quantity and the pressure π ¹).

In this way we have determined several adsorption-isotherms, corresponding to different quantities of CaF_2 on the wall of the glass-bulb. The surface of the CaF_2 -layer is often much larger than the area of the glass, covered by it. Therefore it is impossible to determine the thickness of the layer from the quantity of iodine; but in every case the following relation between the quantity of iodine m and the pressure π must hold:

$$\ln \frac{\pi}{\pi_0} = C \cdot K_2^m,$$

K_2 still depends on the surface (quantity of CaF_2); for one and the same surface, however, it is a constant. Fig. 7 shows an example of such an adsorption-isotherm; it relates to the adsorption on a glass-surface of

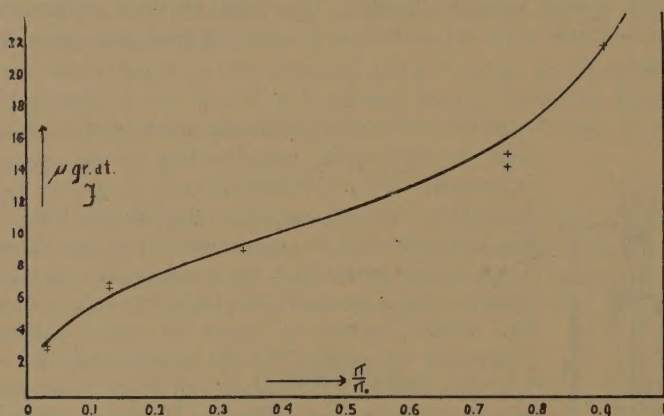


Fig. 7.

about 75 cm², which was covered with about 7.5 mgr. of CaF_2 ²).

In fig. 8 the quantity of iodine m is shown as a function of $\log \left(-\log \frac{\pi}{\pi_0} \right)$. The corresponding points must lie on a straight line. The line, drawn in the figure, has been determined by means of the theory of least squares; before, in view of possible sources of error, different weights had been given to the various points. The line can be represented by:

$$\log \left(-\log \frac{\pi}{\pi_0} \right) = -0,086 m + 0,495.$$

¹) To the measurements and the other results deduced from them we will recur elsewhere.

²) On account of the fact that each point has been determined with the aid of another glass-bulb (the bulbs were as much as possible alike) and also as a consequence of other sources of error, there is always a possibility for deviations in the situation of the points.

On account of the fact that

$$0.495 = \log \frac{\varphi_1}{4.57 T}$$

and because $T = 293^\circ$, it follows from this that

$$\varphi_1 = 4150 \text{ cal.}$$

This figure is of the same order of magnitude as that which was calculated with aid of the considerations given above.

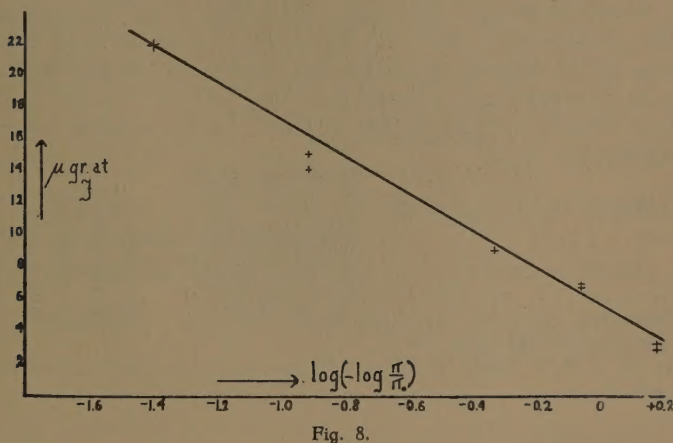


Fig. 8.

In case other quantities of CaF_2 are used, the magnitude of the constant K_2 is different; it appears, however, that the constant C always keeps the same value, exactly as one would expect according to our view.

Our measurements cannot be represented by an adsorption-isotherm of the usual form. A characteristic feature is the rise of the curve, if $\frac{\pi}{\pi_0}$ approaches the value 1. Such a rise in the vicinity of the pressure of saturation has already been observed many times; in such cases, however, this has been ascribed to other phenomena¹⁾.

As already mentioned above, the colour of the adsorbed layer of iodine is brown. In case iodine become polarised to a high degree, we must expect that the absorption-band of the iodine will be shifted in the direction of shorter wave-lengths, as a consequence of which the colour of the iodine changes to brown. We have measured the absorption-spectrum of the brown layer²⁾, and we have found that the absorption starts at about

¹⁾ E. HÜCKEL, in his already mentioned book, ascribes a similar rise to condensation in capillar spaces. We hope to prove later that this explanation cannot be applied to the present case.

²⁾ We like to express also in this place our sincere thanks to Drs. A. VAN WIJK for his help with the measuring of the absorptionspectrum.

6000 ÅU. It increases at shorter wave-lengths, shows a maximum at about 2950 ÅU and then decreases rather rapidly. According to the measurements of L. S. ORNSTEIN and H. C. BURGER¹⁾ the maxima of the absorption for violet solutions of iodine (in carbonsulfide and in chloroform) lie at about 5100 ÅU; in alcoholic solutions the maximum lies at about 4300 ÅU. The maximum of absorption in solutions of iodine in potassium-iodide, according to CH. WINTHER²⁾, at about 3500 ÅU. From these measurements we see that with increasing polarisation of iodine, the absorption-band seems to shift to shorter wavelengths. On account of this we can assume that the polarisation of iodine in the adsorbed layer is larger than in solutions of KI₃. Indeed, also in KI₃ one can imagine the binding of the iodine as a consequence of polarisation³⁾.

I have pleasure in thanking Mr. J. BROOS for his valuable help with the experiments.

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¹⁾ Verslag Kon. Akad. Wet. Amsterdam, **29**, (1920) 573.

²⁾ Z. Phys. Chem. **108** (1924) 236.

³⁾ See Dr. A. E. V. ARKEL. and J. H. DE BOER, Rec. d. trav. chim. d. Pays Bas, **47** (1928) 593.